MANDIBULAR MOVEMENTS AND THEIR CONTROL IN THE WETA, *HEMIDEINA MAORI* (ORTHOPTERA : ENSIFERA : STENOPELMATIDAE)

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ABSTRACT

The peripheral mechanisms involved in the control of mouthpart movements are investigated.

All the behaviours observed to involve the mandibles are described.

The morphology of the head capsule, mandibles, and mandibular muscles are described together with the innervation of the mandible from the suboesophageal ganglion. Myography and morphology are combined to investigate the mechanical functioning of the mandible.

A survey of the mandibular sense organs revealed a number of sensilla associated with the cuticle, and three stretch receptors spanning the mandibular joint. Ultrastructural examination showed two of these to be muscle receptors. The ventral muscle receptor organ (VMRO) is structurally complex. Its physiological responses are strongly dependent on efferent input, including reflexive input from the contralateral VMRO.

Peripheral control in several behaviours was tested. The imposition of loads during inactivity and mastication revealed a load compensating capability. A control mechanism involving the VMRO as an error detector is proposed.

The effect of VMRO ablation on the coordination of feeding and defensive biting was examined. In both of these, precise occlusion of the mandibles was impaired. By inducing defensive biting onto force transducers the bite strength of each mandible was recorded independently.

The right mandible was found to have a dominant role in determining bite duration. The effects of VMRO ablation supported this. Bite duration under these restrained conditions appeared to be limited by the inability of the mandible to close. This again appears to be monitored by the VMRO in an error detector role.

Other effects of ablation on biting are consistent with a position-monitoring function of the VMRO. This appears to involve a system of comparison involving the VMRO from each mandible. The proposed control mechanisms are all explicable in terms of the known receptor physiology.

CHAPTER I

INTRODUCTION

The feeding behaviour and mouthparts of insects have long attracted the attention of biologists with a diversity of interests. This is certainly true of the Orthoptera and the related insect orders characterised by strong, biting mandibles.

Detailed anatomical descriptions of the head and mouthparts of orthopterans began appearing early in the literature (e.g. Börner, 1909; see Snodgrass, 1950 and Matsuda, 1965 for reviews). These constitute a comprehensive account of the structure of mouthpart musculature. While many were largely anatomical descriptions, the functional morphology of arthropod mouthparts has been considered in detail by Snodgrass (1950) and mandibular mechanisms by Manton (1964) to interpret evolutionary relationships. Knowledge of insect mechanisms was extended by Strenger (1942) in her functional analysis of the heads of a broad range of orthopteran groups.

From an ecological approach the relationship between mandibular form and diet has been clearly demonstrated (Isely, 1944; Williams, 1954). Distinctive characteristics have been found in the cusp patterns of carnivorous grasshoppers and those feeding on grasses, forbs, seeds, flowers and combinations of these. Incisor and molar regions are differentiated in response to dietary requirements to the extent that little of phylogenetic value is found in the various mandibulate

patterns (Isley, 1944).

Besides feeding, a diversity of behaviours involving the mandibles has been reported. Antennal grooming in cockroaches is an established undergraduate laboratory preparation. Intense inter-male combat, involving grasping of the legs in the mandibles and head biting, has been described in Hemideina femorata (Sandlant, 1981). Another stenopelmatid species, Stenopelmatus, produces clicking sounds with its jaws (Tinkham and Rentz, 1969, cited in Field and Sandlant, 1983).

The social insects, with the exception of the stem mother aphids, are all mandibulate. Within these groups the range of mandibular activities is extended to nest construction and defence of the colony in termites and ants. Carrying of debris, food and developing young is characteristic of the ants. Brood tending is found in all the groups (Wilson, 1972, gives numerous examples).

Chewing insects, either larval or adult, have caused extensive damage to timber and agricultural crops whether before harvest or in storage. Their economic importance is the impetus behind the intensive research effort into the feeding mechanisms of the Acrididae.

The vast body of literature on the feeding of locusts and grasshoppers can be divided into several categories. Food preference and selection deals largely with dietary composition and chemoreceptive mechanisms (Mulkern, 1967). The control of feeding encompasses the effects of physiological state, such as diapause or moulting, the timing and pattern of feeding, the quantities ingested

as well as the effects on motivation of satiety and starvation (reviewed in Barton-Browne, 1975; Bernays and Chapman, 1974; Bernays and Simpson, 1982).

Investigation of the sensory mechanisms involved has been an integral component of this research. Distension of the foregut by ingested food excites stretch receptors which inhibit feeding behaviour (Bernays and Chapman, 1974). Chemoreceptors are involved in the location of food, its selection and the maintenance of feeding. These are not necessarily mouthpart sensilla, as in Locusta where receptors on the antenna are involved in olfaction. The labrum, hypopharynx, labium and maxilla all bear chemoreceptive sensilla both scattered and in local aggregations, reaching particularly high densities on the maxillary and labial palps (Chapman and Thomas, 1978). Study of these trichoid contact chemoreceptors has reached sophisticated levels with the demonstration of receptor inhibition by hormonal release from the corpora cardiaca following feeding (Bernays, Blaney and Chapman, 1972).

No such statement can be made about any aspect of mandible physiology. Despite all the effort applied to locust feeding the appendages responsible for biting and chewing the food have been largely ignored.

This is in some ways surprising. A recent thrust in invertebrate neurobiology has been the investigation of cyclical behaviour and the interactions between its central and peripheral components (reviews Huber, 1975; Hoyle, 1977). Many behavioural activities are known to be cyclically recurring, e.g. wing movements in flight

or stridulation; leg movements in walking, swimming or stridulation; ventilatory movements of the insect abdomen or crustacean appendages; radula activity in feeding molluscs and mouthpart movements in arthropods. Many approaches have been adopted and current knowledge of insect neurophysiology shows the value of this. Cybernetic analysis has allowed the modelling of insect gaits (Graham, 1977) and the influence of sense organs in the control of leg movements (Bässler, 1977). The structure and physiology of the sense organs is known in some detail for increasing numbers of sense organs (Burns, 1974; Hustert, 1982). Patterns of central connectivity are being elucidated (Burrows and Horridge, 1974) together with the central processing of sensory input (Field and Burrows, 1982).

Against the background of such interest in the coordination of behaviour and in locust feeding the lack of knowledge of mouthpart control seems a major omission. The mandibular functioning of insects presents unique opportunities to the physiologist interested in peripheral feedback. All the activities involving mandibular closure, from the delicate nursery ministrations of the worker ant to the unremitting activity of the wood-boring beetle larva and the aggressive biting of the soldier termite or weta, must surely involve an element of control of two parameters, position and force. For the asymmetrical mandibles to meet appropriately their relative positions must be regulated to ensure that the cusps intermesh. If the forces generated on the two sides are not equal then one mandible will tend to displace

the other, or to rotate the head if a rigid object is being bitten. Moreover the strength of the bite must be adjusted to the task and the balancing of forces maintained whether the mandibles are chewing soft tissue or sustaining a strong, isometric bite. Unlike those of the Apterygota (Manton, 1964) the insect mandibles are not mechanically coupled and have no common adductor elements. All coordination must be achieved by the nervous system. The appeal of this preparation lies in investigating the peripheral mechanisms.

Similar considerations apply to the mandibles of crayfish. While not homologous with insect mandibles, through convergence these appendages have acquired similar functions in the two groups (Manton, 1964). The sense organs of the Homarus mandible include a muscle receptor organ (Wales and Laverack, 1972a,b) which may be part of an error-detecting servo system (Wales, 1976). While Homarus proved capable of some independent movement of the mandibles, these were invariably bilaterally coupled in the normal cycle of rhythmic biting (Wales et.al, 1976b). The pattern altered with changes in the physical nature of the feeding substrate. To account for these results an hypothetical mechanism incorporating position and tension-sensitive afference has been proposed (Macmillan et.al, 1976).

The only insect whose mandibular functioning has been investigated physiologically in any detail is Schistocerca gregaria (Seath, 1977a,b). By imposing cyclical movements of various frequencies on the mandibles, synchronised movements of the other mouthparts were elicited.

Myograms from the mandibular adductors showed bursts of activity at the same frequency as the imposed waveform. The phasing of these in the published records varies considerably and resembles resistance reflexes in a number of instances, although this aspect was not considered. Driving of one mandible usually elicited bursting activity in the ipsilateral muscle only. However, when grass was placed between the mandibles the free closer muscle showed activity similar to that of the driven closer muscle. It was clearly shown that this response could be mediated solely by mechanoreceptors. Evidence consistent with the involvement of receptors in the cusps is presented. When driving the mandibles simultaneously but at different frequencies, Seath (1977a) recorded synchronous myogram activity at the higher driving frequency from both closer muscles. Burst lengths resembled those recorded from the lower frequencies, from which it was concluded that the afference from both mandibles was combined centrally to give a coordinated pattern of motor output.

Schistocerca was shown to alter closer muscle frequency when feeding on relatively incompressible food or when the mandibles were artifically loaded. To account for this, Seath (1977a,b) has postulated a tension receptor providing positive feedback to the closer musculature, although no attempt was made to find an appropriate receptor.

Following ablation of campaniform sensilla on the mandibles, tonic closer muscle discharges were recorded during maintained mandibular opening, whereas phasic

bursts had been found in the intact animal. It was suggested that these sensilla inhibited the closer muscles when tension levels potentially damaging to the mandibles were approached.

In summary, Schistocerca has been shown to coordinate its mandibles closely through unknown peripheral mechanisms. These allow it to maintain chewing activity under different mechanical loadings, as its varied diet requires (Chapman, 1974). Knowledge of the sensory input is largely speculative.

The sense organ complement of insect mandibles has received even less attention from physiologists than the motor functions, although anatomical studies have described both internal receptors and external sensilla from several orders.

Fine canals transversing the cuticle in the cusp regions of mandibles were found to be innervated in Calotermes (Isoptera) (Richard, 1951), Locusta (Le Berre and Louveaux, 1969), and larval Speophyes (Coleoptera) (Corbière-Tichané, 1971). On the basis of light microscopy and presumed contact with food, the sensilla were assumed to be chemoreceptive. An ultrastructural study on larvae of the coleopteran Speophyes (Corbière-Tichané, 1971) showed similar canals associated with scolopophorous organs, and inferred a sensitivity to cuticular deformation from the position of the dendrite within the cuticular canal. A similar scolopidial organ was found in an elaterid larva by Zacharuk and Albert (1978), who also recorded tonic responses to deformation of the mandible with a glass rod. A curious

feature of the response was the stated lack of modulation with alteration of stimulus pressure. None of the tested solutions of various sugars, amino acids or salts elicited any electrophysiological response when applied to the cusp regions. These authors have suggested that pore canal organs in insect mandibles will prove to have a proprioceptive function wherever they are found. Neither of the scolopophorous organs described from mandibles is in a position to monitor the angle of the mandibular joint.

Other mandibular receptors are known only from anatomical descriptions. In an extensive catalogue of the mouthpart receptors of Schistocerca, Thomas (1966) described only the external structures. Three classes of setae, distinguished by their lengths, were found on the mandibles. Although two of these size classes include putative chemoreceptors, the function of the mandibular sensilla is not commented on. Trichoid sensilla have also been noted by Zacharuk and Albert (1978) and Corbière-Tichané (1971, 1973).

Campaniform sensilla have been described from the beetle larvae mentioned above, and from Schistocerca (Thomas, 1966) and Locusta (Le Berre and Louveaux, 1969). They occur in well-defined groups close to the basal margin of the mandibles in the two locusts, although the exclusive use of first instar larvae may not have given a representative picture of Locusta. In Schistocerca, destruction of one of these groups resulted in a tonic myogram discharge from an adductor muscle unit previously showing phasic activity (Seath, 1977a). No other

physiological data on mandibular campaniform sensilla has been published.

No mention has yet been made of stretch receptors of any type spanning the mandibular joint. Three different receptors have been described from the beetle Oryzaephilus (Honomichl, 1978a,b). These three receptors are substantially different from one another and from other proprioceptors described from insects. Two are muscle receptor organs associated with slender adductor muscles arising on the tentorium and inserting into the base of the mandible. The dorsal muscle receptor has a single sensory cell whose nonciliated dendrites ramify between the endings of the two muscle fibres. The receptive region is thus in series with the muscle fibres. The ventral muscle receptor has eight sensory cells, with nonciliated multiterminal dendrites ending in the region of the Z-discs of the receptor muscle and also in a compact cord alongside the muscle. This represents at least one component in parallel with the muscle fibres, while the association with the Z-discs suggests that the dendrites may be in series with the muscle. A similar muscle receptor has been described from the mandible of adult Dermestes (Honomichl, 1976).

The third receptor is a bundle of nonciliated dendrites and supporting glial cells stretched between the anterior arm of the tentorium and the apodeme of the principal adductor muscle. The three sensory somata are grouped beside the receptor strand on the surface of the mandibular nerve. Any movement of the mandible alters the length of this receptor. The physiology of

the three sense organs has not been studied, nor has their role in regulating mandibular activity.

In summary, current knowledge of mandibular sense organs consists almost entirely of anatomical details. The external sensilla are known in selected orthopterans and coleopterans, while ultrastructural details of the internal receptors are known in several larval and adult beetles.

The aim of this thesis was to investgiate mandibular functioning and the control mechanisms involved. Observations of behaviour, muscle anatomy and myography, and sense organ ultrastructure and physiology have been drawn on to provide a broad basis for understanding mandibular activity in a single animal.

The chosen subject was Hemideina maori, an endemic New Zealand species commonly known by its Maori name, weta. H. maori is a large ensiferan orthopteran from the family Stenopelmatidae. Several features make it particularly suitable for the study of mandibular function. The advantages of large size are conferred by the megacephaly and enlargement of the mandibles found in the adult males of many stenopelmatid genera (Beier, 1955; Field and Sandlant, 1983). While these have probably evolved primarily for use in interactions between males (Sandlant, 1981) the mandibles are an awesome component of a defensive threat display and can deliver a painful bite. The threat display, biting and feeding are all readily elicited in the laboratory. The anatomical study of the closely related Hemideina thoracica (Maskell, 1926)

showed mandibular musculature similar to that of other primitive orthopterans (Strenger, 1942; Matsuda, 1965), suggesting that the mechanisms in H. maori may usefully be compared with those from other orthoptera.

This thesis is organised in the following manner. The first of the results chapters surveys all the behaviours involving the mandibles which were seen in a laboratory setting. In general, these observations apply to animals unrestrained by any experimental apparatus. Then follows a detailed examination of the structure of the head capsule and mandibles, and the morphology of the mandibular muscles. The central nervous ganglia in the head are described briefly, with greater detail on the suboesophageal ganglion and the mandibular nerves. The morphological data are then combined with myography in considering the biomechanics of mandibular activity.

Chapter V briefly speculates on the possible peripheral feedback required to achieve the observed performance, and is followed by a survey of the internal and external receptors associated with the mandible. Two muscle receptor organs spanning the joint between the mandible and head capsule are described in ultrastructural detail, together with the physiology of the more complex of these. The role of this receptor in coordination is examined in the final results chapter. In a series of experiments quantifying various behaviour tasks, mandibular activity is monitored before and after ablation of the muscle receptor.

The results from all the chapters are considered in a final discussion.

CHAPTER II

METHODS AND TECHNIQUES

I COLLECTION AND MAINTENANCE OF THE EXPERIMENTAL SUBJECT

Hemideina maori is a subalpine species found above the tussock line in a number of ranges in the South Island of New Zealand. It is nocturnal in habit. By day it can be found in well-aerated and drained spaces under boulders, either in a horizontal prone position or hanging more or less horizontally from the under surface of the boulder. All specimens used in this study were collected from the Rock and Pillar Range near Middlemarch in central Otago. Wetas found here were much larger than others from the same species found in different localities. Above 4000 feet the vegetation was sparse with large areas of exposed rock and smaller stones. On these were many thin, relatively flat slabs of schist-like rock which could easily be overturned. A rock approximately two feet square might shelter up to 12 wetas, often clustered together in contact with one another. The bare appearance of the surfaces beneath the rock and the large accumulations of decaying faeces suggested that the same sites were regularly used. The level of sociality these aggregations represent is unknown. It is possible that their composition varies from day to day. However, one feature is clearly evident. It was unusual to find more than one mature male weta under any rock. If two or more were present they were never in close proximity.

The aggregations consisted mainly of large females, although juveniles of either sex might be present in small numbers.

Not all wetas were found in such large groups. Juveniles and adults of both sexes were found in isolation and groupings of all sizes occurred. It was unusual to find more than two or three juveniles together and large groups of males were not found. These observations apply mainly to the warmer months although collections were also made in mid-winter. Large aggregations were not found on all collecting trips, perhaps reflecting a seasonal variation in behavioural pattern.

Collections were made three or four times per year and the animals stored at 15^{o}C with a 12 hour period of artificial light each day. Housing conditions reflected the distribution pattern described above. Females and juveniles were kept in 9-inch diameter open plastic containers, three or four per container. Mature males were individually housed in lidded plastic containers five inches square. Fierce fighting, frequently resulting in death or gross injury, often occurred between mature males kept in the same container.

A varied diet of apple, cabbage, clover, Melicytus leaves and cooked chicken was readily taken. Growth and moulting of juveniles was sustained and a supply of vigorous animals was available at all times.

II BEHAVIOURAL OBSERVATIONS

Most behavioural observations of unrestrained wetas were made during the early evening on animals in their

usual holding cage in the constant temperature room. Males were housed in larger containers prior to observation. Lighting was from an ordinary 40 watt incandescent bulb. During their normal dark period wetas showed all the commonly observed behaviours, including mating, under well lit conditions, even if their cage was removed to another room for observation. Handling readily elicited threatening behaviour and defensive biting and inhibited feeding for no more than a few minutes after handling in most animals.

All the commonly observed behaviours involving the mandibles - feeding, climbing, threatening and defensive biting - were readily elicited in animals held by the head in a restraining device, described in detail later in the chapter. All quantitative data on mandibular activity was obtained from restrained animals either coupled to a variety of transducers or recorded on 16mm film and analysed frame by frame.

III SKELETAL MORPHOLOGY

The structure of the head capsule and mandibles was investigated using scanning electron microscopy, described elsewhere in this chapter, and light microscopy. Material prepared in several ways was examined under the dissecting microscope and drawn with the aid of a drawing tube. Material was either fixed in alcoholic Bouin's, macerated in 10% potassium hydroxide and all the soft tissue and trachea removed, or else heads were dried and the internal contents scraped out.

Lengths and angles were measured from drawings made with a drawing tube from carefully aligned specimens. Where necessary, a horizontally-mounted microscope was used to determine that structures drawn were all in the focal plane.

IV ANATOMICAL TECHNIQUES

(1) Nerve and muscle anatomy

The investigations of muscle and neural anatomy were made from material fixed in alcoholic Bouin's fixative. The dissected fixed material was drawn using a Wild drawing tube. Details of innervation were supplemented with material stained specifically for the purpose. Dilute methylene blue in weta Ringer (see below) selectively stained nerves in refrigerated fresh preparations. Cobalt chloride was infused from a suction electrode into the cut ends of nerves in fresh preparations. Five percent $CoCl_2$ in 0.013% bovine serum albumen was applied for approximately 6 hours at room temperatures. After washing with Ringer, the preparation was bathed in ammonium sulphide diluted in Ringer for 15 minutes, washed again and fixed in Carnoy's fixative. The preparation was often dissected further at this stage before dehydration in an ethanol series and clearing in cedarwood oil.

(2) Determination of sarcomere length

Measurements of sarcomere length are from material fixed in situ in alcoholic Bouin's and washed in 70% alcohol. Small fibre bundles were then removed from the

muscle, teased further, and the counts made from material temporarily mounted in 70% ethanol. All measurements were from at least a 10-sarcomere length of fibre counted under a compound microscope. Where mean values are quoted they refer to the mean of several such measurements.

(3) Scanning electron microscopy

The scanning electron micrographs were made from material fixed in 2% glutaraldehyde in 0.1M cacodylate buffer (pH = 7.4), critical-point dried and sputter coated with gold. Material was examined with conventional instrumentation and images recorded on 35mm film.

(4) Sense organ structure

The structure of the muscle receptor organs was first investigated with conventional wax histology, using material fixed in alcoholic Bouin's and stained with Mallory's Triple stain.

The ultrastructure of the sense organs was determined from material fixed in 2% glutaraldehyde in 0.1M sodium cacodylate buffer at pH 7.4. The osmolarity of the fixative was adjusted to 480 mOsM with sucrose. The chilled primary fixative was injected into the mandibles of intact wetas which had been cooled for one hour in the refrigerator at 4°C. H. maori is weakly active at this temperature. Immediately after injection was begun the animal was decapitated, the head placed in fixative and a further 5-10 mls of fixative perfused through the mandible from the hypodermic syringe, still in place following the initial injection. After 30

minutes the required tissue was dissected out, still under the fixative. After 4 hours fixation the material was washed in cacodylate buffer (15 minutes) post-fixed in 1% osmium tetroxide in cacodylate buffer (1 hour), dehydrated through an ethanol series and embedded in Spurr's plastic resin.

Sections were cut with glass knives, collected on slot grids covered with either Formvar or celloidin, and stained with Reynold's lead citrate and uranyl acetate. The sections were examined at 100kV using a Jeol 100C transmission electron microscope.

V PHYSIOLOGICAL RINGER

The ringer used in the methylene blue and cobalt backfilling preparations and in the sensory physiology, was derived from the analysis of H. maori haemolymph published by Leader and Bedford (1978). The recipe given below closely approximates the true haemolymph composition in cation concentration, chloride ion concentration and osmotic pressure.

To make one litre of ringer the following salts were dissolved separately and added progressively:

NaCl	1.93gm
KCl	0.41gm
$CaCl_2$ (anhyd.)	0.44gm
$MgCl_2.6H_2O$	2.08gm
$Na_2SO_4.10H_2O$	8.38gm
$NaHCO_3$	0.84gm
sucrose	68.46gm

when buffered to pH 7.2 with 0.02M Hepes, this gives a solution with osmolarity Δ = 475 mOsm.

VI FORCE AND POSITION MONITORING

In all experiments where the force of mandibular adduction or the movement of the mandibles was monitored it was necessary to restrain the animals. Different methods of restraining the animal by the head capsule were used in cinematography and in monitoring with electronic transducers.

(1) Cinematography

For the cinematography the animals were held by two perspex blocks 5-6mm across attached to the sides of the head capsule with cyanoacrylate glue. Several days after these were in place they were waxed to two metal rods by which the animal was restrained.

The animals were filmed with a Bolex 16mm camera using Kodak Tri-X film forced to 400 ASA. Lighting was provided by two fibre optics sources giving a high light intensity but no heat. Animals fed readily under these conditions, allowing recording free from the influence of transducers.

The mandibles were spotted with white paint to act as reference points. The film was analysed frame by frame when projected onto graph paper and the displacement of the reference points measured.

(2) Restraining device used with transducers

In all other position and force monitoring

experiments the wetas were restrained with a moulded cast fitting onto each side of the head capsule. The basic moulds were cast from Vertex Dentimex dental cement using a mature male head capsule as a model. Each cast was glued to a quarter-inch brass rod which slid into a plexiglass block, where it could be fixed with a grub screw. The blocks were screwed onto a flat plexiglass base which was in turn screwed onto the steel baseplate of the steady bench (Figure 2).

Each experimental subject was lightly anaesthetised with CO_2 and the head capsule fitted as closely as possible into the case without using any pressure. The cast was then loosened slightly and liquid polycarbamate dental cement poured in between the cast and the head capsule. This cement flows readily into crevices and conforms closely to the contours of both the head capsule and the cast. No adhesive bonding is involved. Unlike many cements it sets without releasing heat. In some experiments this case was loosened when set and cyanoacrylate glue run down between the cast and the head capsule. The cast was then retightened, gluing the head to the cast. For this bond to be effective the waxy layer was removed from the cuticle with fine sandpaper.

Despite this elaborate procedure the mounting sometimes loosened towards the end of experiments where a lot of attack-biting was produced. This was because the head capsule altered shape when extreme forces were produced (see Chapter IV) particularly in unilateral biting.

(3) Apparatus used to record bite strength

The strength of mandibular biting was measured with rigidly-mounted Grass FT-10 force transducers. These gave an output of approximately 700μV.kg^{-1}. Exact values were determined from a calibration curve. The recorded value varied with the distance of the point of contact of the transducer coupling from the articulation. This has been compensated for by expressing bite strength as torque (gm.cm) the product of the measured force times the displacement of the transducer coupling from the anterior articulation.

The output of both force- and position-monitoring transducers was displayed on a high speed oscillographic recorder. Bite durations were measured at a chart speed of 25mm.sec^{-1}.

(4) Mounting and coupling of the force transducers

In the experiments where the force of mandibular adduction was measured the transducers were rigidly mounted to restrict mandibular movement as much as possible. Nevertheless the mounting and coupling to the mandible possessed sufficient adjustments within three planes to control the degree of mandibular opening and to minimise any forces tending to deflect the mandible from its normal plane of action. Each was bolted to a sliding brass plate held onto a heavier brass plate by two screws, (B, Figure 1). Guides on either side of the baseplate restricted the sliding movement to one dimension. The two screws could be tightened to prevent any movement. The precise

orientation of the sliding axis could be determined by altering the alignment of the brass baseplate where it was bolted to the steady bench (Screw A, A′ Figure 1).

Each mandible was inelastically coupled to the force transducer by a piece of brass welding rod. Soldered on one end of this was a brass washer cut into a horseshoe shape. Across the gap was a short length of wire onto which the mandible bit (Figures 1, 2).

The welding rod was attached to the force transducer via a piece of brass shim which permitted the force transducer to be deflected in the horizontal plane. This allowed either coupling to be removed during a biting sequence, and also allowed the coupling to locate in the same cusp each time. Minor adjustment where the shim bolted to the transducer allowed slight repositioning of the transducer coupling in the vertical plane. Contact between the mandible and the transducer coupling was maintained solely by bite force. Abduction of the mandible was completely unrestricted.

This apparatus was used in all force determinations except those testing for possible cusp receptor input. In these, a fine fish hook was inserted through two holes drilled near the tip of the mandible. The hook was connected to the transducer with a fine chain (Figure 2) thus permitting mandibular abduction as with the more rigid coupling. Unlike the welding rod, the chain stretched elastically and the hook opened slightly with each bite. To control for this, force readings were also taken with the hook looped over the cusps, providing contact equivalent to the solid coupling.

The position of each mandible was precisely controlled during the force-monitoring experiments. The head was positioned within the cast so that the axis of rotation of each mandible was as close to vertical as possible, the plane of movement then being approximately horizontal. Before any experimentation the resting position of the mandibles was determined from drawing the head using a drawing tube.

A reference position for each mandible was determined using a graticule eyepiece in a dissecting microscope. One edge of the graticule was aligned between the two anterior articulations (Figure 3). Using the sliding adjustment of the force transducer mounting, the mandible was opened until the tip coincided with one of the vertical axes of the graticule. By measuring x and y coordinates of the mandible tip, the angle of opening could be precisely determined. A micrometer reading of force transducer position was then taken.

Vernier calipers adjusted under the microscope were used to measure the distance (r) from the anterior articulation to the point of contact between the mandible and the force transducer coupling (point C). As this radius was constant, angular displacement from the reference position could be calculated by measuring the linear displacement of point C along the x-axis. This was done with great precision using a micrometer to monitor change in position of the force transducer. The micrometer was mounted on the brass baseplate of the transducer assembly and measured directly from the binding post of the force transducer.

The linear displacement of point C along the x-axis was assumed to be equal to transducer displacement, neglecting the displacement along the y-axis. The y-axis displacement is achieved through slight deflexion of the transducer coupling at the brass shim. As the distance from this point to the point of mandibular contact was large (72mm) compared to the x displacements (3mm maximum) and the angles involved were no more than 25^{o}, the error introduced by this approximation is less than 1% for a position change of 6^{o}. There was no loss of precision in relocating the mandibles for further trials in the same position.

The apparatus allowed very precise control and measurement of the relative positions of the two mandibles. Alterations in position could be nicely determined and earlier positions re-established exactly.

(5) Position monitoring

A flexible, elastic coupling joined each mandible to a sensitive force transducer (Grass FT-03). Any movement in the mandible produced a proportional force in the rigidly-mounted transducer. A brass wire was soldered onto a screw fitting the terminal post of the force transducer arm, forming an extension of the arm along the same axis. This assembly was mounted directly above the mandible with the wire extending vertically downwards to contact the lateral face of the mandible. At its free end the wire was bent into a partial loop, giving a curved bearing surface.

To counteract friction-induced noise resulting from

Figure 1

The experimental apparatus used in the determination of mandibular bite force.

Two transducers were used simultaneously, one coupled to each mandible. The complete assembly for the left mandible and the coupling to the right are shown. Alignment of the longitudinal axis was altered at screws A, A′. Displacement of the transducer along this axis, and thus the degree of mandibular opening was adjusted at screw B. Both flexible chain and rigid welding rod couplings are shown.

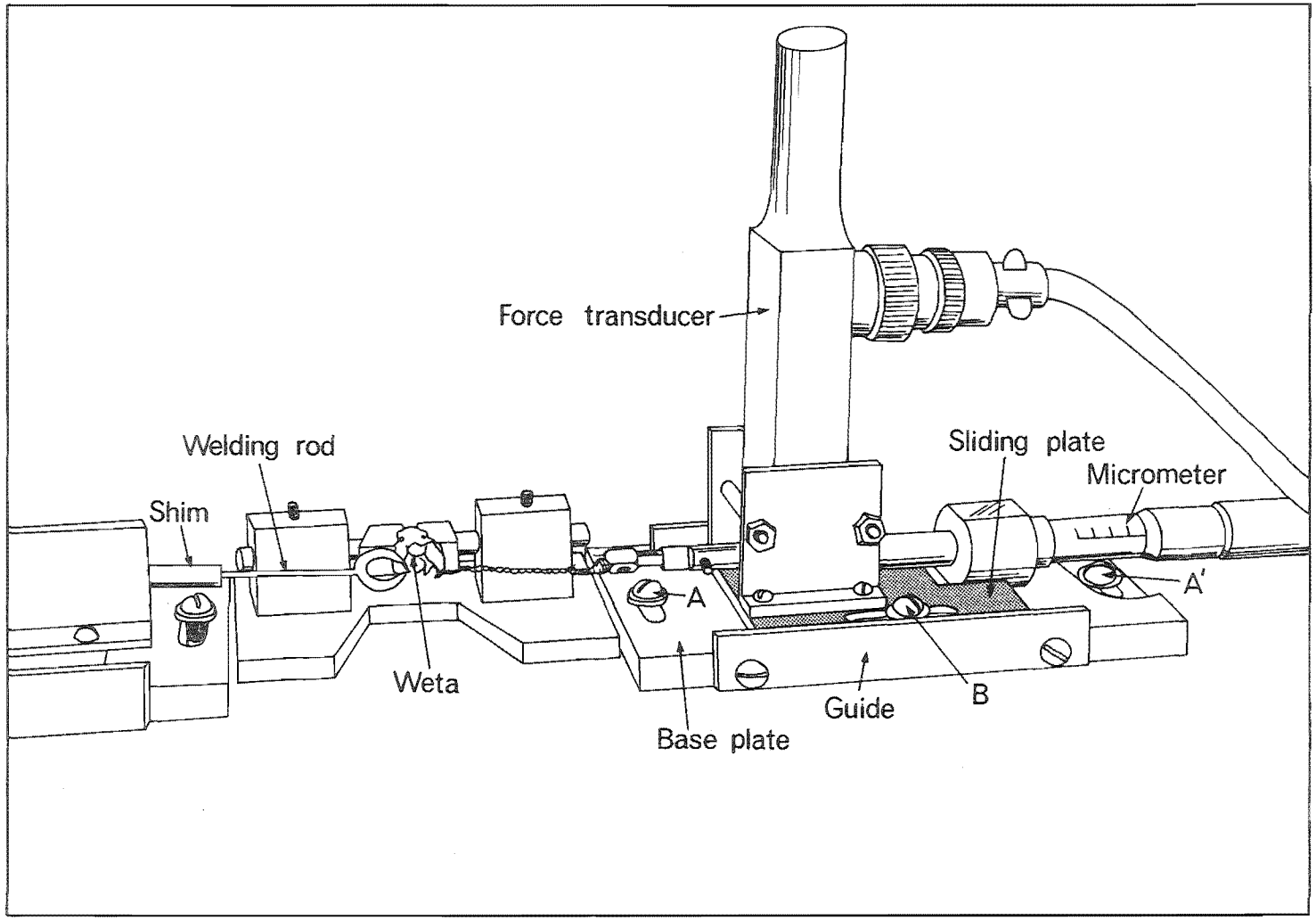

Force transducer
Welding rod
Shim
Sliding plate
Micrometer
A
A'
Weta
Base plate
Guide
B

Figure 2

The restraining device used in the monitoring of mandibular position, in the measurement of bite strength and in the sensory physiology.

The two types of coupling used in torque measurement are illustrated, the solid coupling on the right mandible, the hook and chain on the left. The cut away area of the base plate allowed VMRO ablations to be performed when the whole device was inverted.

CC - cement cast, PC - polycarbamate cement.

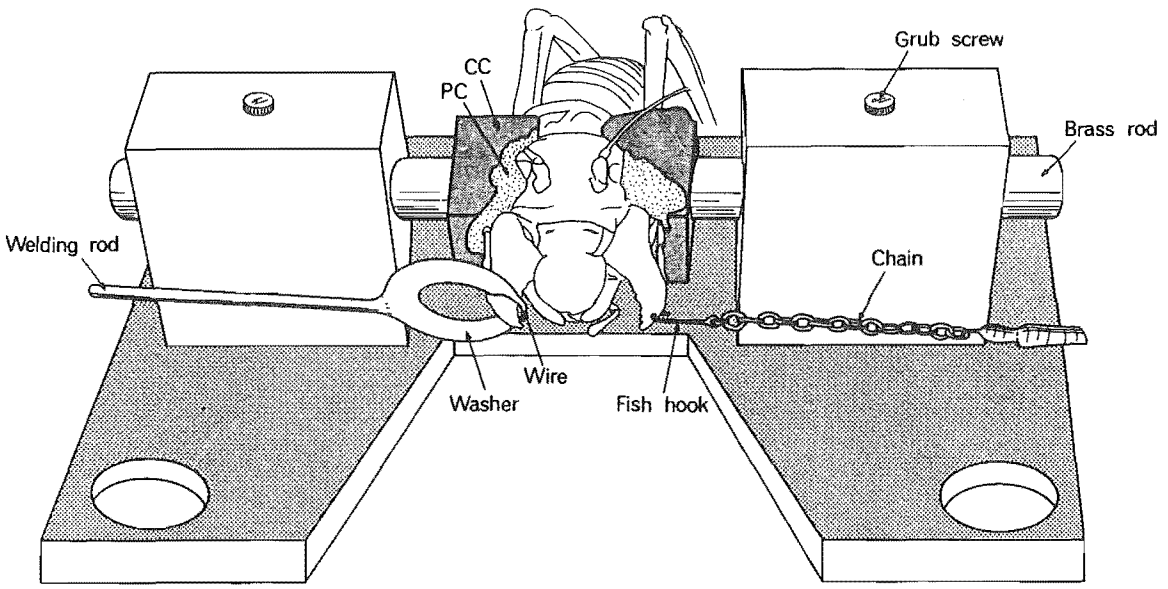
Figure 3

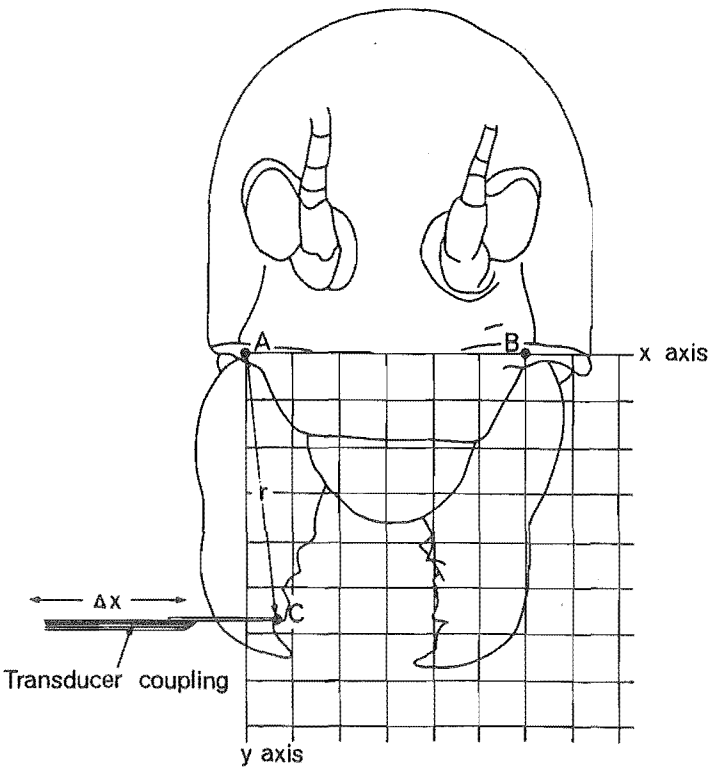
Determination of mandibular position when measuring bite strength.

The eye piece graticule is shown as it appears when aligned with one edge on the anterior articulations (A,B) of the two mandibles.

C - the contact point between the transducer coupling and the mandible.

r - the distance of point C from the anterior articulation.


Grub screw
CC
PC
Brass rod
Welding rod
Chain
Wire
Washer
Fish hook


A
B
x axis
r
Δx
C
Transducer coupling
y axis

direct contact with the irregular mandibular cuticle, a bearing surface was constructed. A 2mm length of polyethylene tubing was split longitudinally and attached to the mandible using polystyrene glue. This glue has proved less toxic to Drosophila than Loctite cyanoacrylate. The half tube was oriented with its long axis vertical, approximately $1\frac{1}{2}$mm from the mandibular hinge. A small quantity of petroleum jelly was placed in the tube. The force transducer was positioned so that a minimal signal was recorded when the wire was located in the tube while the weta was quiescent. Mandibular abduction generated an increasing voltage.

VII ABLATION OF THE VENTRAL MUSCLE RECEPTOR ORGAN

Ablation of the VMRO involved releasing the distal end of the receptor from its insertion on the mandible.

The operation was performed under CO_2 anaesthesia without the animal being removed from the head cast. The entire restraining device (Figure 2) was unscrewed from the base plate, inverted and reattached. The cut-away portion of the front of the device left sufficient room for the ablation to be performed.

The cuticle immediately distal to the TM-1 insertion scar was thinned with a dental burr in an area of several square millimetres The thinned portion was then cut away with a fine scalpel, releasing both the TM-2a muscle and the VMRO, but leaving muscle TM-1 intact. The hole was then sealed with soft dental

wax to prevent bleeding.

No data was collected for at least three hours following each ablation, although testing animals from 15 minutes to 24 hours after anaesthesia showed no obvious differences in defensive biting.

A post mortem examination of each experimental animal was made after fixation in alcoholic Bouin's.

VIII ABLATION OF CAMPANIFORM SENSILLA

Only the distinct group of campaniform sensilla lying between the mandibular margin and the TM-muscle insertion were ablated. A dental burr was used to abrade the cuticle in and around the darkened area where the sensilla are most numerous. This operation was performed under a dissecting microscope after inverting the restraining device in the same manner as for VMRO ablation. The success of the operation was determined by examination under higher power during the post mortem.

IX ELECTROPHYSIOLOGY

(1) Myography

Electromyograms were obtained from the principal adductor muscles (M-21) by single-ended recordings using fine insulated copper wires inserted through the cuticle of the head capsule. The indifferent electrode was a single silver wire inserted through the frons as far away from the mandibular adductor muscles as possible. The cuticle was thinned with a dental burr and a small

hole pierced with an insect pin. The wires were waxed in place.

The myograms from the tentoro-mandibular complex were obtained from fine tungsten electrodes. These were electrolytically etched in a solution of NaOH and $NaNO_2$ before coating with polyurethene varnish. After baking in a $70^{o}C$ oven for at least 24 hours the tip insulation was removed by passing current through the electrode in saline solution. These electrodes were press-fitted into hypodermic needles, and manoeuvred by conventional micromanipulators. Recorded signals were fed into AC-coupled preamplifiers and displayed on a variety of oscilloscopes. Stored traces were copied on polaroid film. Continuous recordings of longer sequences were obtained using a Grass C-4 kymograph camera. Recording from the tentoro-mandibular complex required a dissected preparation. A less extensively dissected variation of the sensory physiology preparation was used. Lesser amounts of both mandibular and head capsule cuticle were removed. The animals were restrained as for the measurement of bite strength.

(2) Sensory physiology

The restraining device employed in sensory recordings was the same as that used in the force determination experiments (Figure 2), with the exception that during the dissection and some of the recordings the mandibles were held apart by a perspex block.

The dissection was carried out under CO_2 anaesthesia.

The clypeus and that part of the frons below the level of the antennal bases were thinned with a dental burr before being cut through with scissors to remove the labrum and most of the cuticle between the two anterior articulations. The newly exposed basal portion of the mandible was similarly thinned and cut away. The anterior arm of the tentorium was then pared down. Careful removal of fatty tissue at this stage revealed the origins of all the muscles in the tentoro-mandibular complex (muscle M-25) as well as mandibular nerve trunks II and III and their finer branches (Figure 32). More proximal portions of all three major nerve trunks were exposed by removing the overlying portions of the hypopharynx.

Bleeding sometimes interfered with recording and could be controlled by ligaturing the dorsal blood vessel between the head and thorax, and by cutting the thoracic cord at the same level. The preparation was periodically bathed with the ringer described above.

As most of the cuticle between the two anterior articulations was removed, there was little to support the head capsule if a powerful bite was produced. Sensory recordings could not therefore be made during forceful biting. Nor could they be made during substantial mandibular movement as all nerve trunks were displaced by the movement of the M-21 apodeme over which they lie (Figure 17).

En passant recordings of sensory activity were made with paired fine silver hooks and fed into an

AC-coupled differential amplifier. Recording with insulated tungsten needles and suction electrodes was used to a limited extent. Signals were displayed on either a Tektronix 5111 storage oscilloscope and recorded on polaroid film, or on a Telequipment oscilloscope and photographed with a Grass C4 camera. The short retention time of the phosphor led to underexposed nerve spikes which have been retouched in some figures. The tops of spikes were dotted with a 0.18mm lettering pen under a dissecting microscope at X10 magnification. Lines were later ruled from the dots to the baselines and thus appear as monophasic deflections on the final figure. Deflections were imposed on the mandible using a hand-operated Narashige micromanipulator mounted on a magnetic base. A fine wire probe contacting the cusp region made the coupling. Displacements were determined using the graduated scale on the manipulator and the resultant angle of opening calculated trigonometrically.

CHAPTER III

BEHAVIOUR

Before attempting a detailed examination of the hardware subserving specific motor tasks I wish to consider the variety of activities which this apparatus can accomplish. These descriptions were condensed from observations of 72 animals over a period of 14 months. All observations were made in the laboratory, usually during a 2-3 week interval following collection.

The repertoire of behaviours involving the mandibles extended well beyond the expected food-processing function. In addition to biting off portions of food and subsequent mastication, ingestion of water was accomplished by the mandibles in concert with the other mouthparts. If approached by the experimenter, a weta of either sex exhibited a complex threat display involving stridulation, postural changes and wide gaping of all the mouthparts. Handling at this stage caused the threat to give way to powerful and protracted defensive biting. If held but unable to bite the weta struggled vigorously with the mandibles continually active in a distinctively erratic manner. Threatening and biting were also features of intraspecific interactions, being shown by both sexes but particularly the males. Other agonistic encounters involving mandibular contact between females were observed. A further possible communication behaviour was the sound production

achieved by mandibular rasping in adult males.

I FEEDING BEHAVIOUR

Examination of the gut contents of Hemideina maori suggested that other insects, particularly beetle larvae were a normal component of the diet. In captivity, cultured Tenebrio larvae were vigorously taken. The mandibles were widely gaped during prey capture but the initial attempt to secure a larva was made with the maxillae, followed immediately by biting with the mandibles. The shearing action of a single bite could sever a larva. After several rapid bites, up to 2-3 per second in the most active animals a more regular mastication followed. Smaller amplitude bites continued at a reduced frequency, between 1-2 per second, until the food was ingested. By this time an unrestrained weta had often begun searching for more food, testing both the air and the ground with its maxillary palps while walking rapidly with frequent turning movements in the vicinity of the last prey capture.

Apple was also taken readily but without eliciting such heightened activity. The more measured rhythm of chewing revealed features in common with the pattern for live prey. The inert food was first grasped in the maxillae while smaller pieces were bitten off. Starting from a wide gape the two mandibles closed in synchrony until they met near the midline. The left then held its position while the shorter right mandible continued to close, creating a shearing action at the

Figure 4

A. Mandibular displacement during feeding on apple.

The position of the mandibles as determined from frame-by-frame analysis of cinematographic records. The zero value denotes the "rest" position for each mandible. The mandibles overlap at this point.

The upper trace of each pair is the left mandible.

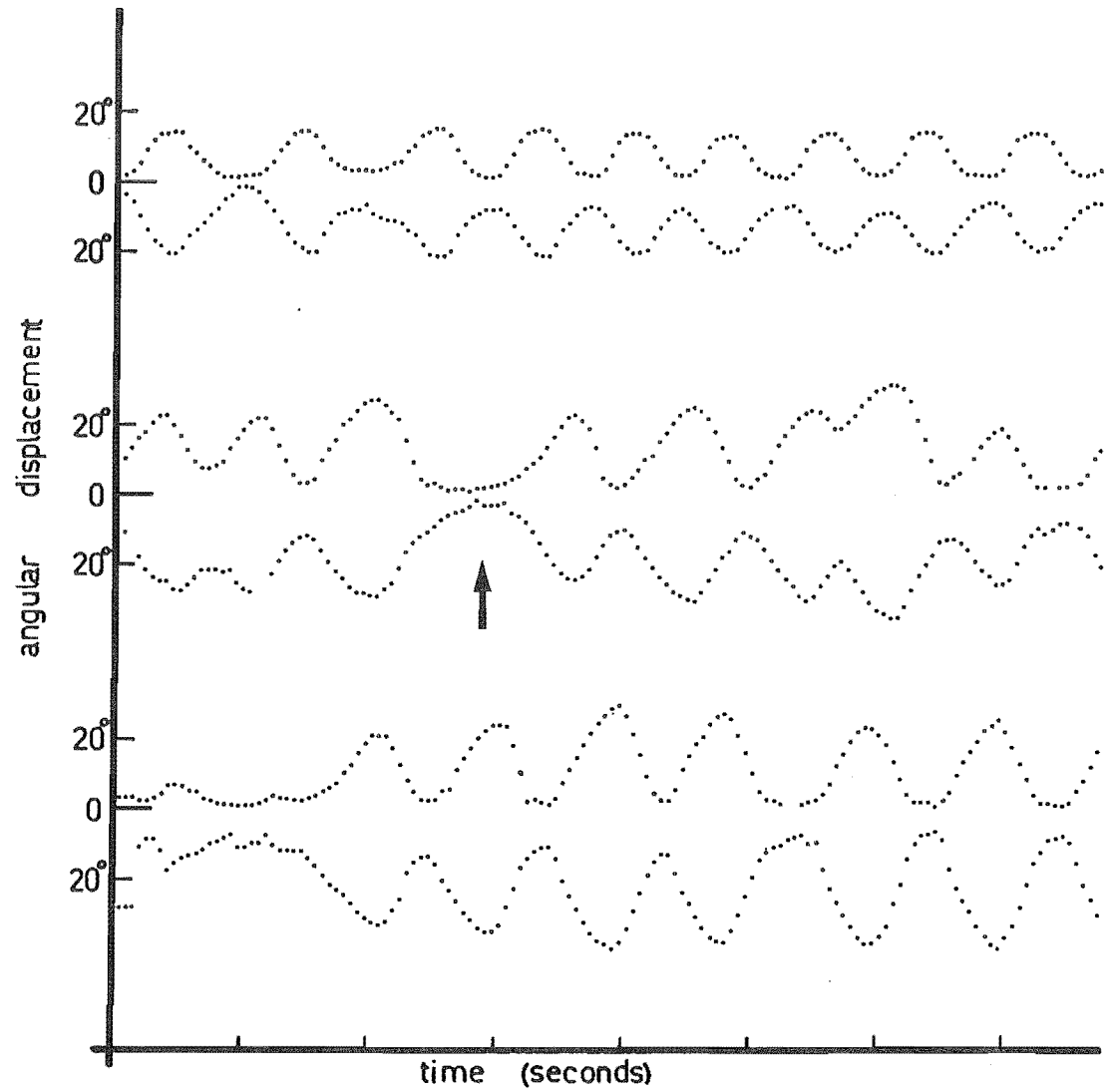
Top trace: mastication of a small portion of apple after it has been bitten off from a larger piece, and is held completely within the mouthparts.

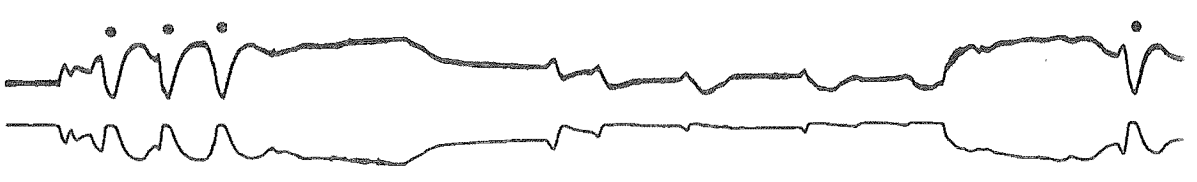
Middle trace: biting into a larger piece of apple held in forceps. The arrow indicates a biting-off manoeuvre.

Lower trace: mastication with a weight attached to the right mandible to produce a constant load. A 17.6gm.cm moment acts in the abduction sense.

B. Threatening and defensive biting in an animal held in the restraining device.

The "rest" position for each mandible is given by the steady level at the beginning of each trace. The right mandible is the upper trace. Defensive bites are indicated by dots. Calibration, 5 seconds.


20°
0
20°
20°
0
20°
20°
0
20°
angular displacement
time (seconds)



more distal cusps. This can be seen in the first two bites in the upper trace (Figure 4) but is more obvious in the records of feeding in Figure 39. Complete or partial closures continued until a smaller portion of food had been detached. Prior to ingestion the food was masticated by the more proximal mandibular cusps. The smaller amplitude and marginally higher frequency of the masticatory pattern are shown in Figure 4A together with a biting-off sequence. The third trace shows a chewing sequence with the right mandible loaded by a 16 gram force acting in the direction of abduction. While opening velocity was increased the frequency was altered little and a co-ordinated bite achieved despite the asymmetrical loading. These traces show that the amplitude and frequency of movement may vary with the task (biting off versus mastication) but that peripheral influences are not the sole determinant of bite pattern. The extra loading had little effect in comparison to the motivational change when feeding on Tenebrio.

II DRINKING

Although H. maori can obtain all its required water intake from its food, a water-stressed weta would drink if sufficient water was available. The distal portions of the mandibles, labrum, maxillae and labium were immersed in the water and made low amplitude cyclical movements at about one third mastication frequency. If defensive regurgitation was then induced

the egested fluid was clear, unlike the more usual opaque brown fluid, demonstrating that water had been ingested.

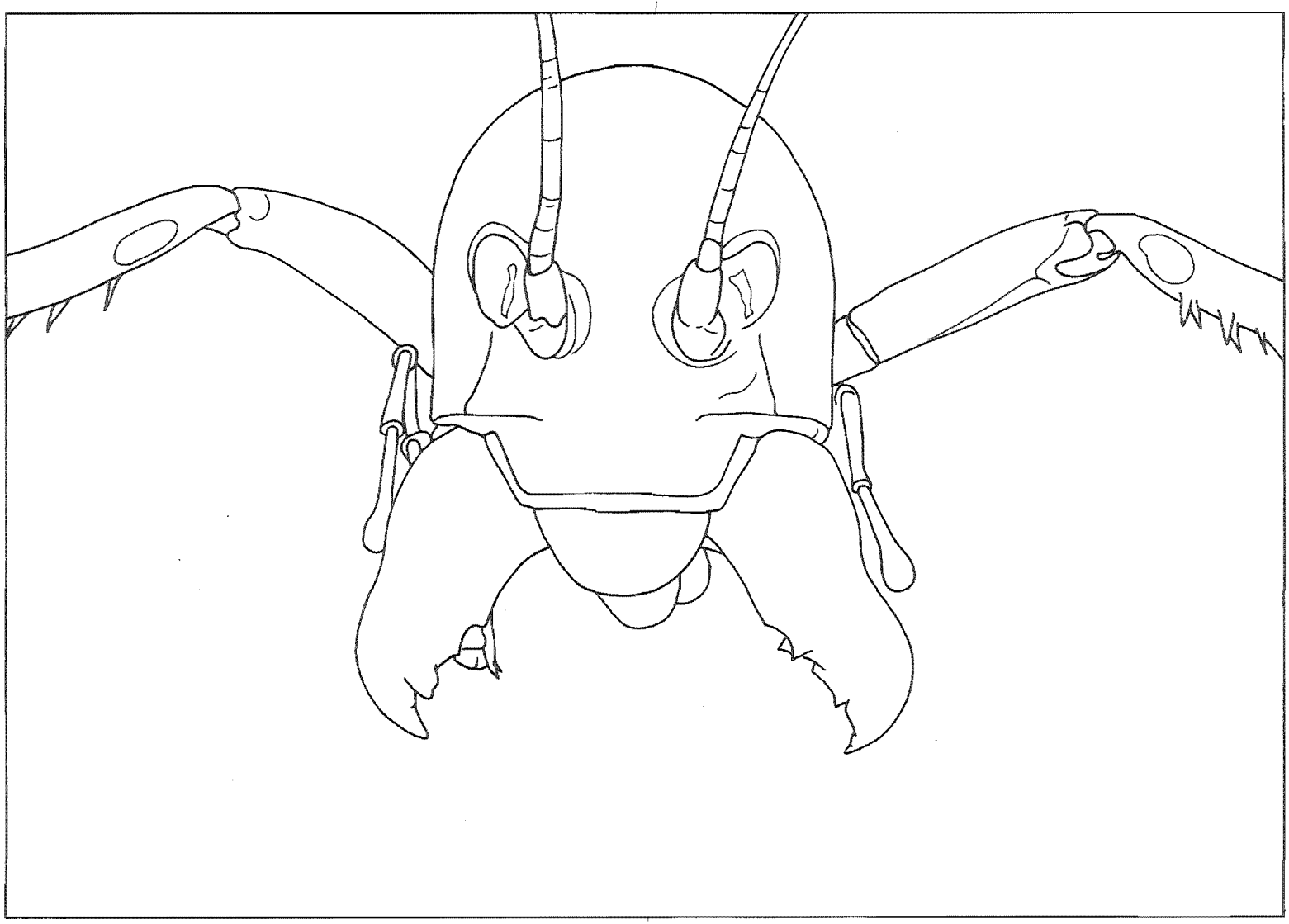
III DEFENSIVE DISPLAY AND BITING

Mandible gaping is a major component of the elaborate defensive display of the weta. In its extreme form the animal flipped itself into a supine position with the legs widely extended (Figure 5). In conjunction with retraction of the labrum, labium, hypopharynx and palps the maxillae and mandibles were gaped widely. Opening angles of 45^{o} from rest position were reached in this graded response. In large males the resulting gape exceeded 13mm, measured at the mandible tips. The smaller females had lesser gapes but the same angles of opening were achieved. Precise measurement of the apparently symmetrical display showed that extreme opening was not reached simultaneously on the two sides. A greater response was not developed on the side from which the noxious stimulus was coming, all measurements being taken from restrained animals. Measuring extreme angles of opening from the rest position gave mean values of 38^{o} and 36^{o} for the right and left mandibles ($n = 15$). The extreme values were attained only briefly (<0.5 secs) and wider opening was usually maintained only during continuous provocation. A plot of mandibular gaping on a restrained animal (Figure 4b) shows habituation of the response after 5-8 seconds but a partially-gaped posture might be maintained for more than a minute following stimulation with a paintbrush.

Figure 5

Mandible gaping.

The widely-gaped mandibles are shown in an adult male weta lying in the supine position, a common defensive posture for Hemideina maori. Drawn from a photograph.



A few brief biting movements normally completed return to the rest position.

A sequence of rapid bites may interrupt the sustained threat posture. These defensive bites began from the widely gaped position and reached full closure as little at 0.2 seconds later. These were the most rapid of all mandibular movements and angular velocities of $150^{o}.sec^{-1}$ were recorded. Biting often occurred when the stimulus was out of range, whereupon the threat posture was rapidly resumed (Figure 4). If an object was caught between the mandibles, a different pattern resulted. A forceful closure of 2-3 seconds duration was followed by a period of relaxation when tension was reduced without the object being released. Several cycles of this pattern could follow before the object was released up to 15-20 seconds from the first bite. Hard objects, such as pencils were released more readily than more compliant materials such as fingers and gloves. Any attempt to free the object during the relaxation phase immediately provoked more forceful biting.

IV STRUGGLING

When held in the hand, and sometimes in the experimental apparatus, the weta struggled vigorously. The legs, antennae and mouthparts were continuously active. The erratic mandibular movements were unsynchronised and of irregular amplitude and duration. The two mandibles might close together with the right overlapping the left, thus preventing contact between all except the terminal

cusps. They were not co-ordinated with the other mouthpart movements, allowing ready detection of struggling behaviour appearing occasionally in feeding sequences.

The lack of synchrony shows there is little mechanical coupling between the mandibles.

V FEMALE-FEMALE INTERACTION

An agonistic encounter of unknown function was very frequently observed between females which were kept in the same container. The most obvious components were the interposing of the widely-gaped mandibles and the occasional incomplete biting movements. During this each animal was palpated about the head and mouth-parts by the other. Bouts of this activity lasted for up to half a minute and were terminated by one animal walking away. In one instance the second female pursued the first and initiated a further similar interaction. This sequence was repeated a second time before the second female ceased to follow the first. The behaviour was quite distinct from defensive or threat displays but its function is unknown.

VI SOUND PRODUCTION

Adult male wetas produced sounds by the forceful abrasion of one mandible against the other during complete closure. The sounds were clearly audible at more than 10 feet distance in the laboratory.

CHAPTER IV

THE MORPHOLOGY AND MECHANICS OF THE MANDIBLE

This chapter begins by describing the skeletal structure of the head capsule and mandibles, including the differences between males and females. The muscles associated with the mandible are described in detail, together with the major nerve ganglia and the innervation of the mandible. The biomechanics of biting are then described. The chapter concludes by examining myographically the activity of the muscle groups under different conditions relevant to the experiments in Chapter VII.

I SKELETAL MORPHOLOGY

(1) The head capsule

An adult male weta in an alert stance is shown in Figure 6. The head is held off the substrate and tilted so that the mouth parts are forward of the rest of the head. When at rest in the prone position the head is rested on the substrate with its long axis horizontal. This strongly prognathous condition contrasts with that of locust in which the long axis of the head is vertical and the mouthparts below the head capsule (hypognathous). In the weta the frontal regions are not always anterior to the occipital regions. In the following descriptions the term "frontal" is used in a broader sense,

denoting those parts of the head and the surface of the mandible shown in Figure 7a.

Frontal and occipital views of the head of an adult male are shown in Figure 7. The mouthparts are typically orthopteran, one exceptional feature being the size of the palps, particularly the elongate maxillary palps. The eyes appear frontally directed, but as the head is tilted upward during activity the field of view is extended above the animal. When the head is held horizontal during rest, the field of view above the animal is extensive.

The head capsule is broad and appears flattened as it is relatively compressed along the fronto-occipital axis. This applies particularly to the male. The dimorphism between the sexes, which shows particularly in the appearance of the head capsule and mandibles, will be dealt with in more detail below.

The ability to bite strongly shows in the development of sulci and heavy tanning of parts of the head capsule. The anterior tentorial pits are clearly evident but the epistomal sulcus which runs between them and delineates the clypeus and frons on many orthopterans is not evident externally. Instead the cuticle in this region is extensively thickened and heavily tanned. The subocular sulcus, running from the eye toward the anterior articulation is present as a raised ridge. This region and the subgena are also heavily sclerotised and the deep subgenal sulcus indicates a well-developed internal strengthening ridge.

Figure 6

A male Hemideina maori in the normal alert stance.

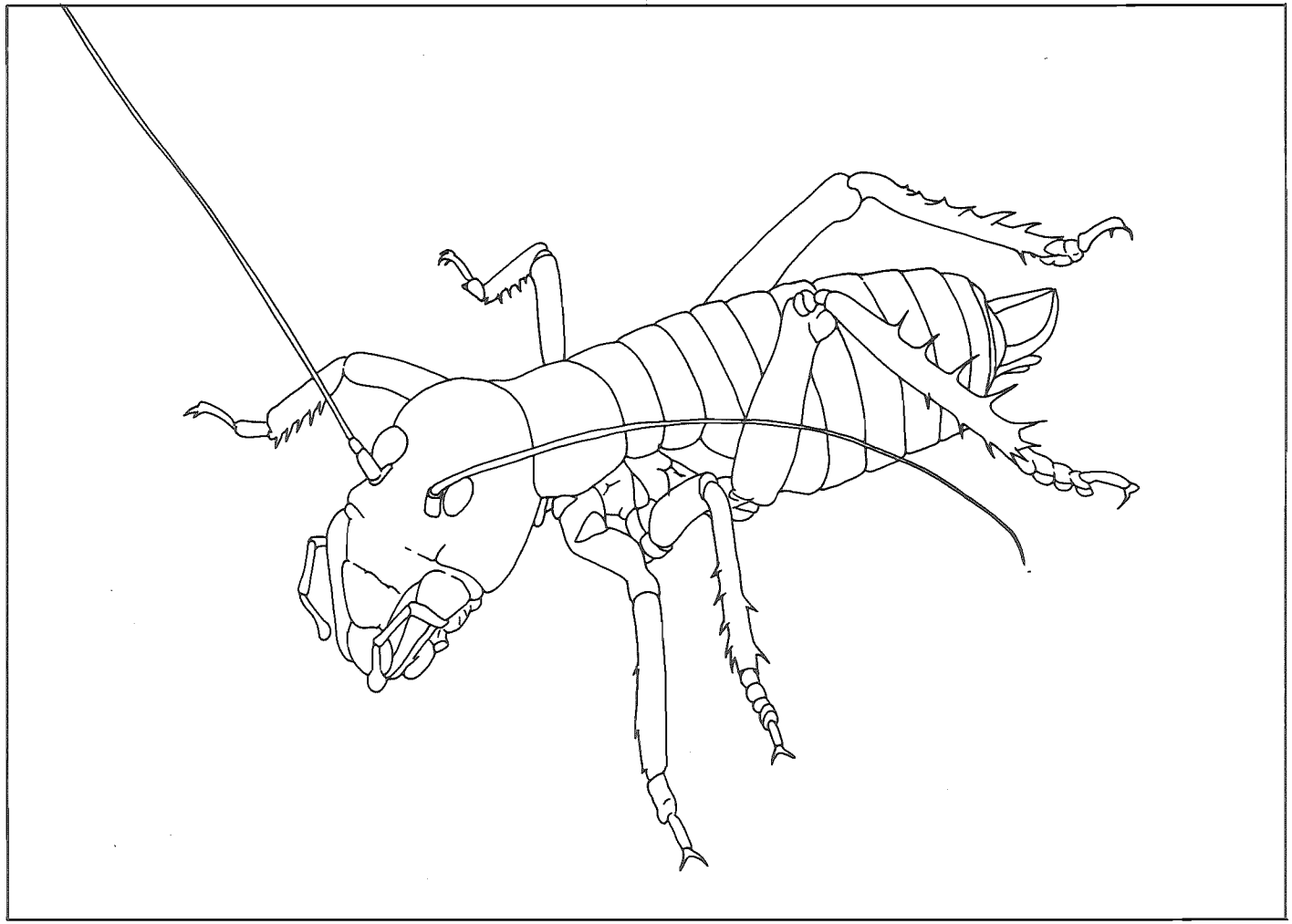
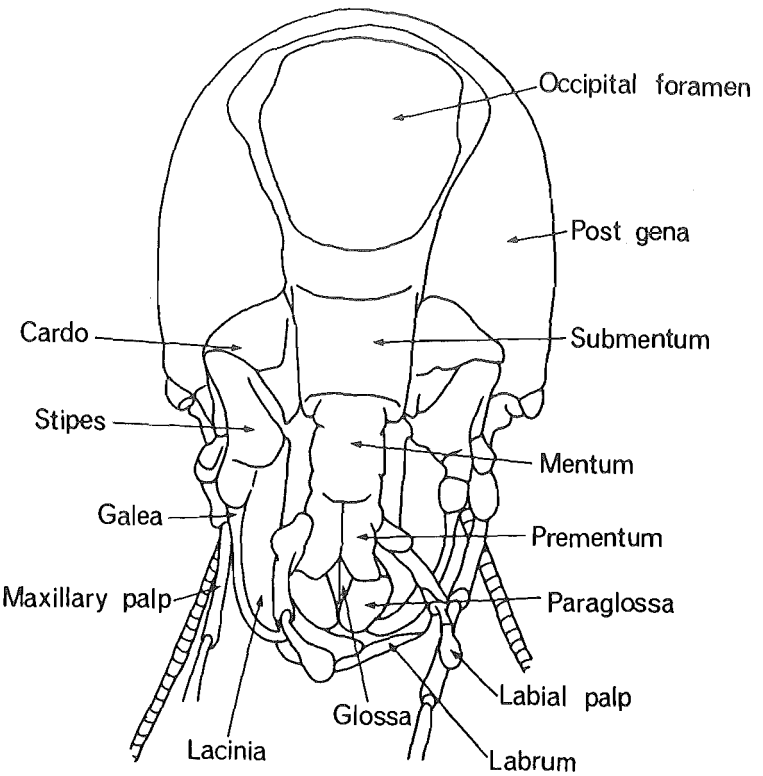


Figure 7

The external anatomy of the head of a male *Hemideina maori*.

(b) Occipital (postero-ventral) view.

(a) Frontal (antero-dorsal) view.


Occipital foramen
Post gena
Cardo
Submentum
Stipes
Mentum
Galea
Prementum
Maxillary palp
Paraglossa
Labial palp
Glossa
Lacinia
Labrum

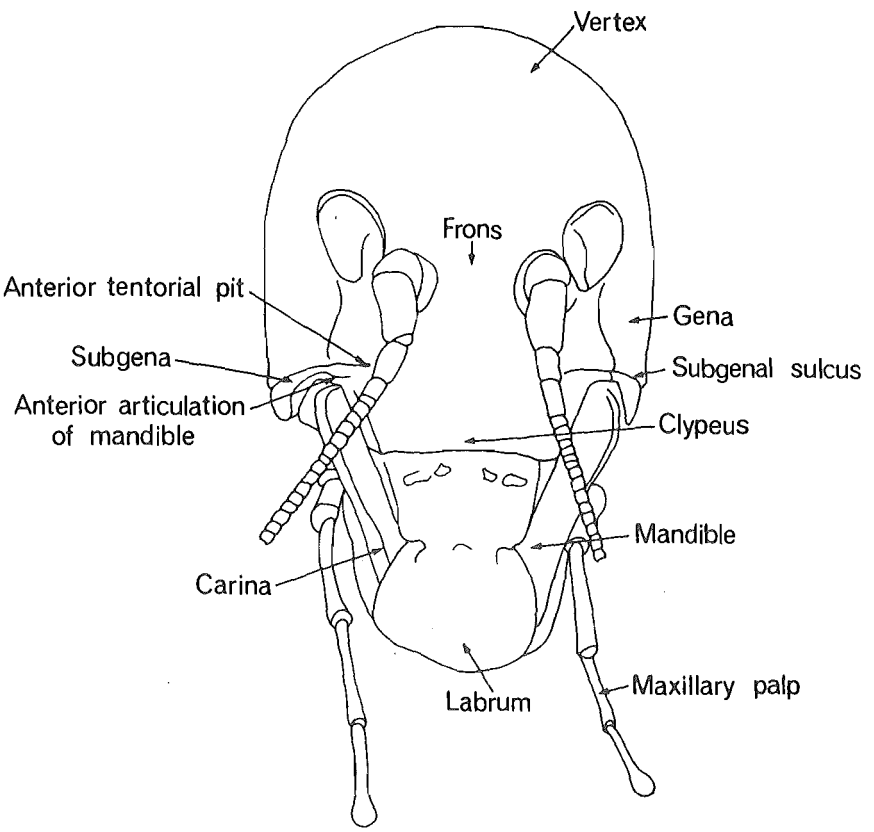
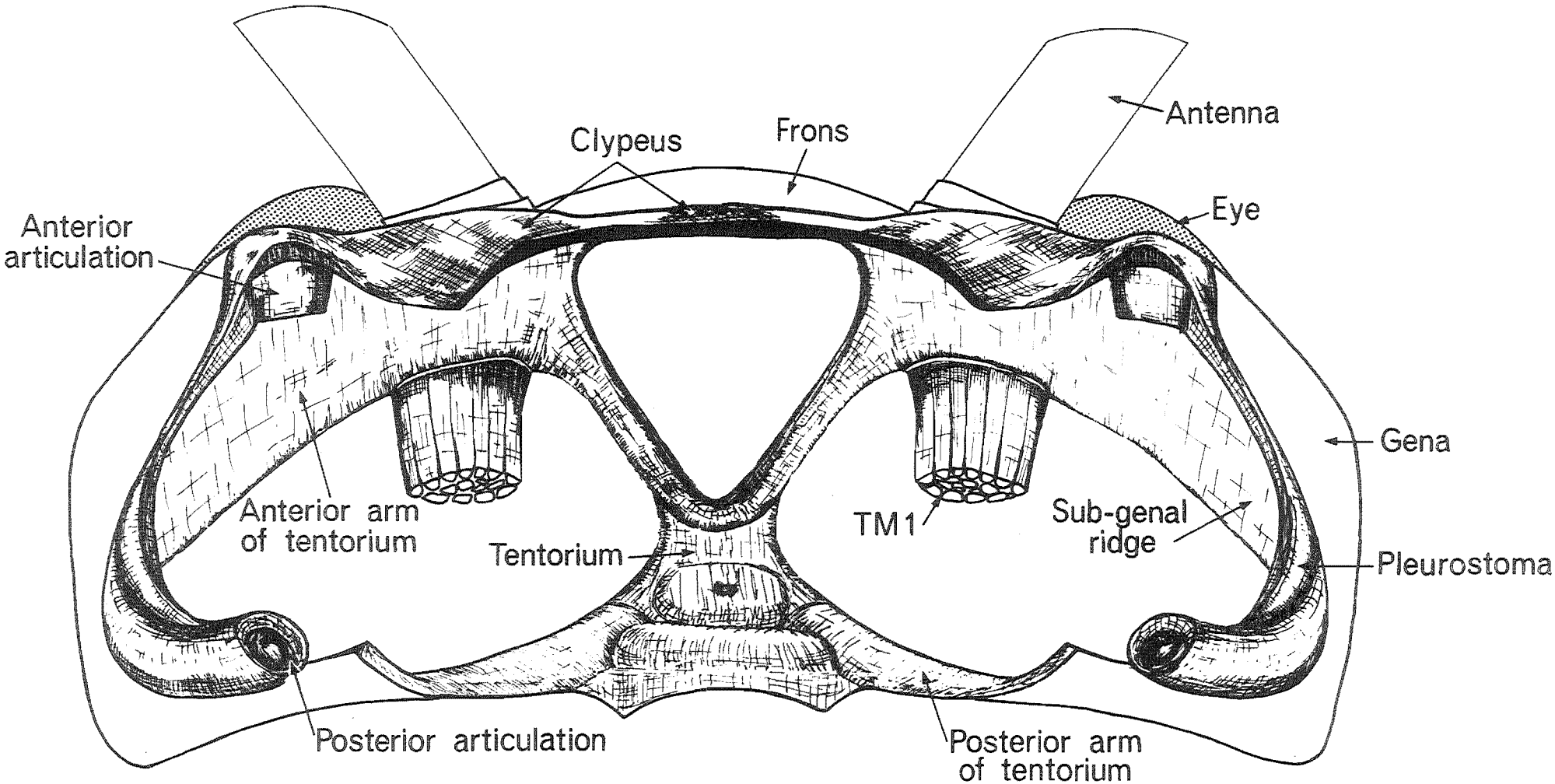

Vertex
Frons
Anterior tentorial pit
Gena
Subgena
Subgenal sulcus
Anterior articulation of mandible
Clypeus
Mandible
Carina
Labrum
Maxillary palp

Figure 8

View of the head capsule with the mouth parts and soft tissue removed to show the structure of the tentorium and its relationship to the mandibular articulations. The proximal portions of the largest tentoro-mandibular muscles (TM-1) are included to show their origin.


Antenna
Clypeus
Frons
Eye
Anterior articulation
Gena
Anterior arm of tentorium
TM1
Sub-genal ridge
Tentorium
Pleurostoma
Posterior articulation
Posterior arm of tentorium

(2) The tentorium

The tentorium is well developed in the weta and performs several roles in mandibular functioning. The anterior arms are large and run continuously into the subgenal ridge forming a strong bracing between the two articulations on each side and also strengthening large parts of the frontal region (Figure 8). They are also sites of attachment for the tentoro-mandibular adductor muscles. The posterior arms are short but continuous with the post-occipital ridge. These latter structures provide attachment sites for muscle bundles from the mandibular adductor muscle, AM-21. The position of the tentorium within the head capsule is shown in Figure 16.

(3) The mandibles

The mandibles are large and elongated. They may exceed 12mm in length in an adult male with a head length of 26mm. They are seen in differing views in Figures 9 and 11. The tips are curved in towards the midline and the medial surface of the distal half of the mandible is a heavily sclerotised cusp region. The mandibular base is approximately triangular with well-developed articulations at two of the angles and the apodeme of the main adductor attaching at the third (Figure 20). The posterior articulation has a ball-and-socket configuration, although it does not function as a universal joint. A round, cuplike depression is formed on the head capsule and a spheroidal projection of the mandible (Figures 10a,b) is held in this by the

action of the mandibular muscles. An SEM view of the posterior articulation is shown in Figure 36, Chapter VI. The articulation can be readily dislocated and abrasion patterns on the mandibles suggested that the left posterior articulation might be dislocated during full strength, complete closures. The anterior articulation is also a loose attachment, but of a different type known as a ginglymus. A heavily-thickened and sclerotised U-shaped collar on the mandible bears against a short, pillar-like surface on the head (Figures 10d,e,f). The two bearing surfaces do not fit exactly and extensive scoring is evident in Figures 10e,f. Muscular action holds the two surfaces together and the two articulations restrict the mandibular movements largely to one plane. The axis of rotation, determined by the two articulations, is known as the hinge line. Between the two articulations on the lateral margin of the mandible, a small protuberance receives the abductor apodeme just lateral to the hinge line (Figures 11, 13a). In contrast the apodeme of the principal adductor muscle, M-21, is widely displaced from the hinge line, giving it a large mechanical advantage. The two articulations and the adductor apodeme insertion are at the three angles of the triangular base of the mandible. The rigid adductor apodeme attaches to the mandible via a flexible zone of untanned cuticle which extends around the basal margin giving a large attachment area and a flexible hinge (Figures 13b, 20).

The mandible tapers from the base to the tip and becomes circular rather than triangular in cross section.

As it does so the mandibular carina gradually disappears. The carina is a prominent feature of the adult male mandible. It begins immediately adjacent to the anterior articulation (Figures 7a, 10f) and extends along the fronto-lateral margin of the mandible as an extended, sclerotised ridge. It reinforces a region under compression during biting but also increases the width of the mandible without influencing the position of the articulations or other attachment points, suggesting that it may have primarily a display function. The dark tanning may enhance signalling efficacy rather than add mechanical strength. On the posterior or ventral surface of the mandible is an indentation with ridges in the cuticle corresponding to the insertion of the tentoro-mandibular muscle, TM-1 (Figure 10a).

A ventral view of the mandible base also reveals a large sclerotised protuberance, the molariform process, on the inner angle of the mandible, adjacent to the M-21 apodeme insertion (Figure 10a). This structure was found only in mature males and is described later in the section on sexual dimorphism.

The mandible tapers and curves so that the extreme tip points medially, approximately at right angles to the long axis of the mandible. The two mandibles are not symmetrical. The left is always longer and overlaps the right in all activities, as is the case in all orthopterans studied (e.g. Isely, 1944). In addition the heavily sclerotised cusps on the distal half of each mandible have a complementary interlocking pattern. The asymmetries in cusp pattern produce an

Figure 9

The cusp patterns of the mandible, illustrated from a male weta.

(a) Left mandible.

(b) Right mandible.

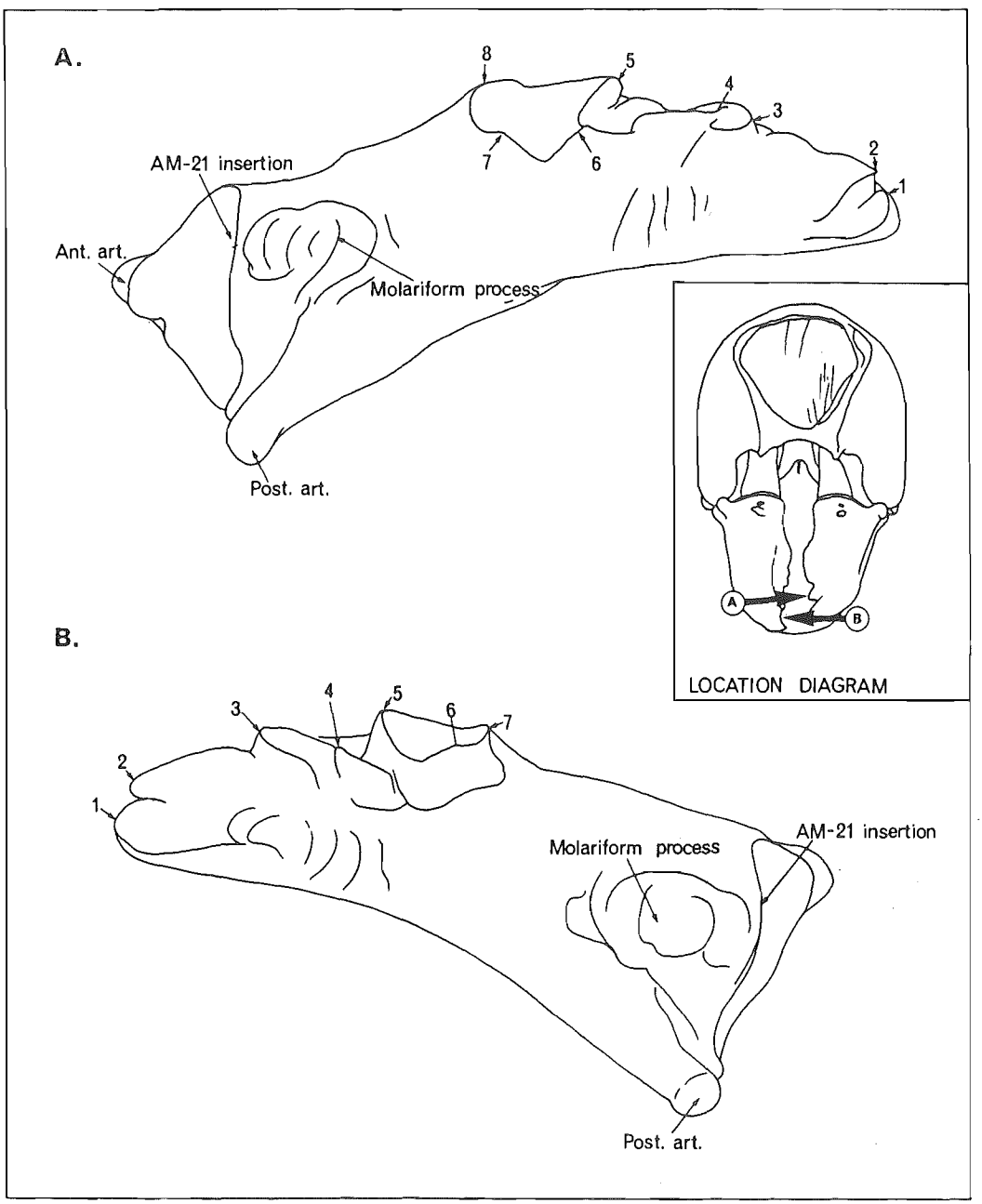

A.
8
5
4
3
2
1
7
6
AM-21 insertion
Ant. art.
Molariform process
Post. art.
A
B
LOCATION DIAGRAM
B.
1
2
3
4
5
6
7
Molariform process
AM-21 insertion
Post. art.

Figure 10

Scanning electron micrographs of a male mandible.

(a) The basal region of the mandible, showing the posterior articulation and the molariform process on the inner margin.

X12

(b) The head capsule portion of the posterior articulation.

X63

(c) The distal cusp region of the right mandible, showing thegosis.

X16

(d) The head capsule portion of the anterior articulation, showing the abraded post onto which the mandible bears.

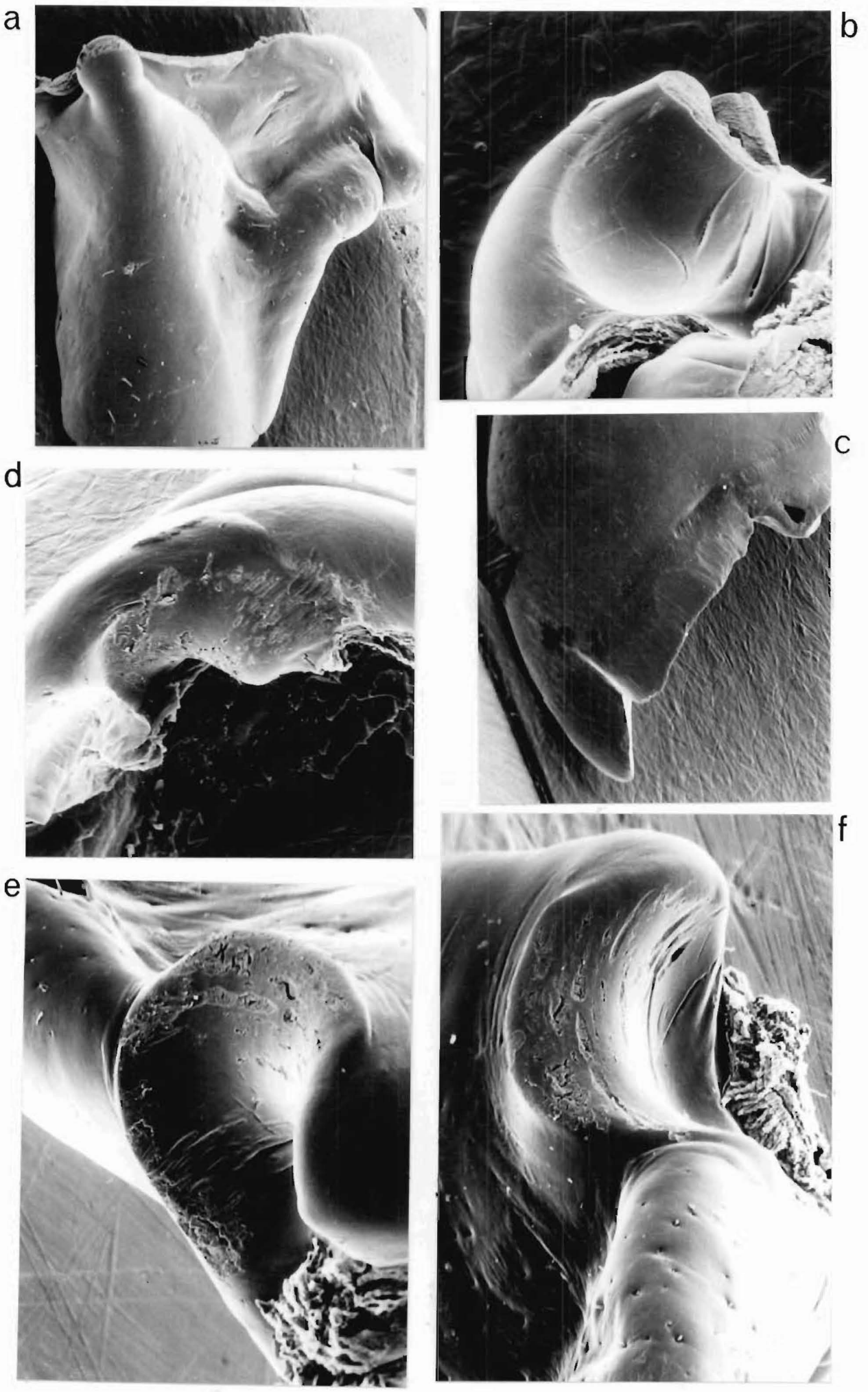
X37

(e) The mandibular portion of the anterior articulation.

X64

(f) The anterior articulation and proximal end of the carina.

X52


a
b
c
d
e
f

efficient shearing mechanism at the distal cusps with the more proximal cusps performing a molar function.

(4) The mandibular cusps

Despite the superficial dissimilarity between the mandibles of adult males and females the pattern of cusps is essentially the same in both. The left mandible differs slightly from the right. Distally the left mandible has two cusps, one slightly sub-apical (numbers 1 and 2, Figure 9). The division between the two may be emphasized by grooves resulting from the abrasive action of the right mandible. The inner face of these cusps forms the surface against which the first two cusps of the right mandible cut in a shearing action. The sub-apical cusp (number 2) and cusp 4 are both elongated ridges lying parallel to the mandibular axis. Cusp 3 has a crescentic ridge. These four cusps overlap corresponding cusps of similar shape on the right mandibles and together form a shearing mechanism used to bite off smaller pieces of food prior to mastication.

The effectiveness of the cutting action of the distal cusps is improved by the continual sharpening of the cutting edge. Abrasion of one face of the cusps by the action of the other mandible leaves a sharpened edge, most noticeably on the right mandible (Figure 10c). Here the outer, or frontal, face of the cusp is abraded as the shorter, right mandible closes inside the left. The outer surface is convex while the inner is concave, so that a sharp edge is maintained by the abrasion. This process is analogous to the thegosis described

from mammals (Every 1970) where an effective cutting edge on the teeth is maintained by wear on one side of the tooth only. Thegosis was most evident in adult male wetas.

The proximal cusps, four on the left and three on the right mandible, together form a crushing unit used in mastication. While their function is that of the molars in mammals, the mechanism is different. The rigidity of the hinge permits minimal lateral displacement, insufficient for the grinding action of two surfaces sliding past each other. In the weta the proximal cusps form a system of intermeshing cones, ridges and depressions in which food is held and crushed. On the left mandible cusps 5 to 8 surround a central depression with papillae in its centre. Cusp 5 on the right mandible fits into this depression. Cusps 5 to 7 on the right mandible also surround a depression containing papillae (Figure 38, Chapter VI), which receives cusp 7 from the left mandible. The possible sensory or mechanical functions of the papillae are unknown. The more direct abuttal of these cusps leads to wear on their points and the ridges between them may be scored away. All the cusps are very heavily sclerotised, this process beginning even before ecdysis is complete. A newly-moulted H. maori is a pale blue-green colour from a haemolymph pigment, except for the eyes and the mandibular cusps, which are black.

(5) Sexual dimorphism

Like all other members of its genus, Hemideina maori

exhibits a pronounced sexual dimorphism. While the sexes can be readily distinguished by the presence or absence of the elongate ovipositor, and the abdomen of the female is longer and often more distended, it is in the head that the differences between the sexes are most obvious. Only in mature animals are the differences apparent. Juvenile animals of the two sexes can be distinguished only by their genitalia. The practised observer can with difficulty distinguish a male in the last nymphal stage from a female by head capsule structure alone. With the final moult to maturity a male develops a head which is larger than the female's, differs in shape and colour, and has unique morphological features associated with the mandibles.

The head capsule is both longer and broader than in the female, without the third axis (fronto-occipital) increasing in the same proportion. The head thus appears larger and more flattened. The various sulci and strengthening ridges are more strongly developed, particularly in the region of the anterior articulation.

Heavier and more extensive tanning markedly alters the appearance of the male head. All the frontal and parietal parts of the epicranium with the exception of a few small regions on the frons, are tanned to a dark reddish-brown, tending to black in the strengthened regions. In females and immature males the cuticle above muscle origins is tanned brown and the regions in between are a much lighter yellowish colour. The heavily-reinforced regions are brown, not black. The post-genal regions, not readily visible in intact

animals, are not heavily tanned in either sex. The colour differences extend to the mandibles which are much more heavily tanned in the males, most of the parts visible in the intact animal appearing black, a colour found only on the cusps in females.

While the cusp pattern is the same in both sexes, the mandibles of mature males differ in morphology as well as colour. The carina extending from the anterior articulation along the fronto-lateral margin has already been described. This structure is peculiar to adult males. It may have a structural function supporting the mandibles which are longer and subjected to greater forces than occur in juveniles and females. Irrespective of this, the carina increases the width of the mandibles without substantially changing their volume. A signalling role seems probable and may be the exclusive function of this heavily-tanned structure.

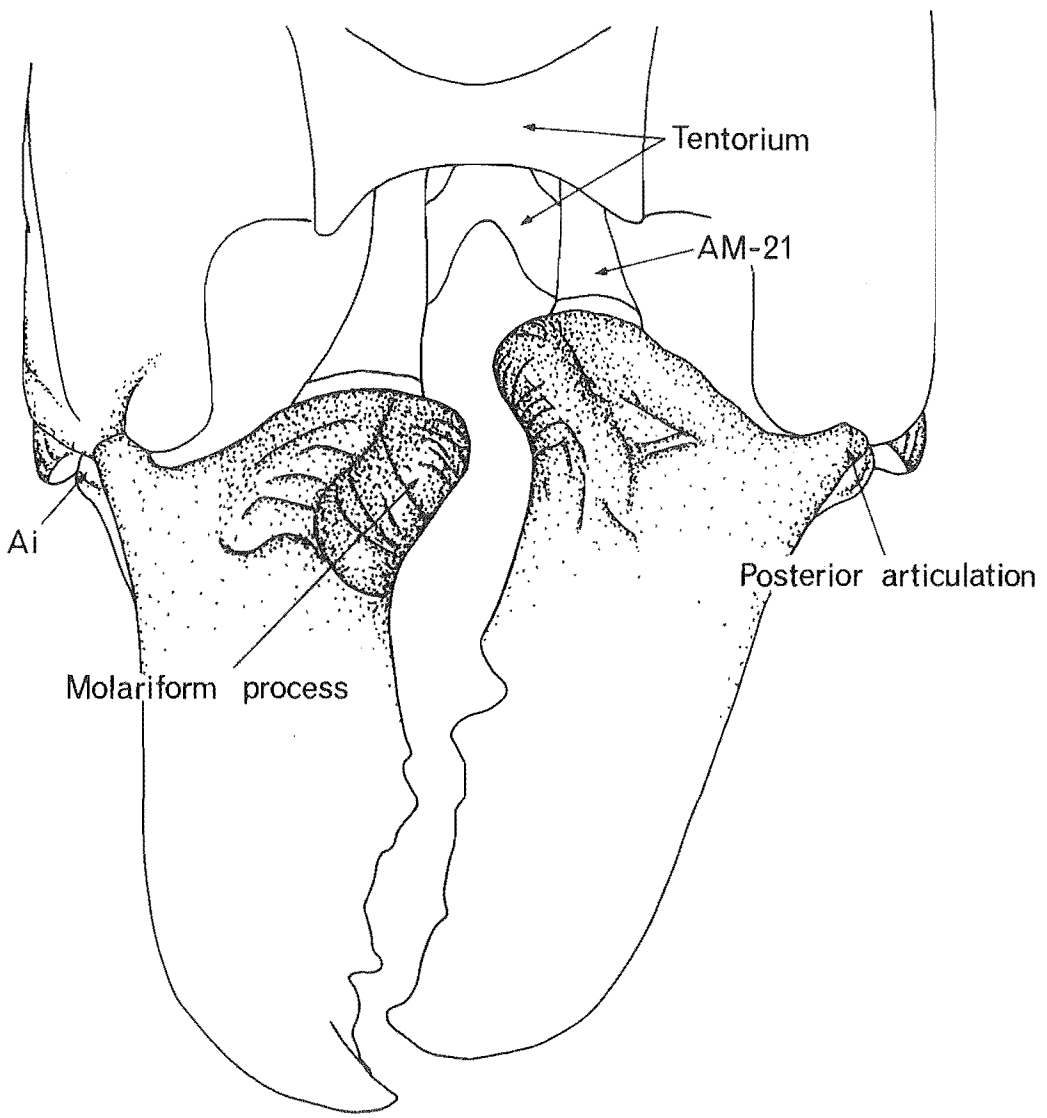
A similar conclusion applies to another exclusively male structure. With the final moult the adult male gains a large protruding structure on the inner margin of the base of each mandible (Figures 10a and 11, compare Figures 14 and 36). These strongly crenulated and heavily sclerotised protuberances have been termed molariform processes because of their resemblance to molar teeth. It is unlikely that they are involved in the mastication of food. They lie behind the mouth and the other mouthparts cannot readily manipulate food in this region. The two processes do not project far enough to contact each other, although cusp contact is often not an essential aspect of mastication. They

Figure 11

Posterior view of the mandibles of a male weta.

Ai - insertion of the abductor apodeme.

Am-21 - apodeme of adductor muscle M-21.


Tentorium
AM-21
Ai
Posterior articulation
Molariform process

show no sign of wear or abrasion. Except when fully retracted in the threat display, the hypopharynx extends between them. In short, they are not well situated for masticating food. A role in feeding would imply a dietary difference between adult males and the rest of the species. None is evident in laboratory feeding, and insect and plant fragments have been recovered from the gut contents of both sexes (R.S. Bigelow, pers. comm.).

In other species of Hemideina examined (H. femorata, H. crassidens, H. ricta) the adult male had similar structures not found in females or juvenile males. Considering the different habitats and predominantly vegetarian diet of these species, together with the data already presented, any involvement in feeding for the molariform processes seems most unlikely. Their restriction to adult males suggests a role either in mating and associated behaviour, or in encounters between adult males. Observation of numerous mating attempts failed to reveal any involvement of these structures in either a signalling or a grasping function. Nor did they appear to be involved in grasping during fighting between males.

In the mandible gaping component of the threat display the hypopharynx is fully retracted and the molariform processes are clearly visible. Mandible gaping is a feature of encounters between wetas, particularly males. The blackened processes may have a signalling function. The sclerotisation may simply be to blacken the structures for visual contrast rather

than to strengthen them for mechanical reasons. This does not explain the prominent ridging.

Another possible function is strengthening the basal region of the mandible. The M-21 adductor muscle apodeme attaches to the mandible very close to the protuberance. While the cuticle in the attachment region is more heavily tanned in adult males the shape of the molariform process does not appear to confer structural support.

The function of the sexual dimorphism of the head is not clear and the differences may well result from both behavioural and mechanical constraints. Larger head size and darker colouration may have a signalling function but may also result from the need to increase the strength of the adductor muscle in order to compensate for increased mandibular size.

II MUSCLE MORPHOLOGY

Four distinct muscle groups can be identified in the weta mandible. These have been described using the numbering system of Matsuda (1965).

(1) Muscle 21 (M-21)

This tergal adductor, which inserts on an apodeme arising from the inner basal angle of the mandible is the largest muscle in the weta. While it is not the sole adductor it is much the largest. The combined bulk of M-21 from both mandibles occupies most of the volume of the head capsule. Most of the dorsal epicranium

above the level of the antennae serves as an origin for the tergal adductors, including the vertex, gena and occipital regions (Figure 12). Bundles of fibres also arise from the postocciput and the posterior arms of the tentorium (Figures 12b, 14). Certain fibre bundles from M-21 in the two mandibles share a common origin (Figure 13b). They arise from opposite sides of a thin process protruding asymmetrically from the postocciput (Figure 14). As this process is firmly attached to the epicranium it does not constitute a transverse tendon linking the two mandibles. Rather, it is a means of expanding the available area for muscle attachment and of equalizing the distribution of muscle bundles about the axis of the M-21 apodeme. This would reduce the net lateral forces acting on the apodeme. While it is possible that fibres sharing the common origin may be active simultaneously for mechanical stability, this would be the limit of mechanical coupling between the two mandibles.

The sites of muscle origin are indicated on the head capsule by darker tanning. The resulting pattern is roughly bilaterally symmetrical, the two sides being similar but not equal. This pattern does not reflect the underlying muscle structure accurately. Both right and left muscles have bundles originating on the opposite sides of the midline, the bundles from the two sides interdigitating. This results in a more even distribution of forces around the apodeme axis. The area of right M-21 insertions to the left of the midline is greater than the corresponding area of left insertions to the right

Figure 12

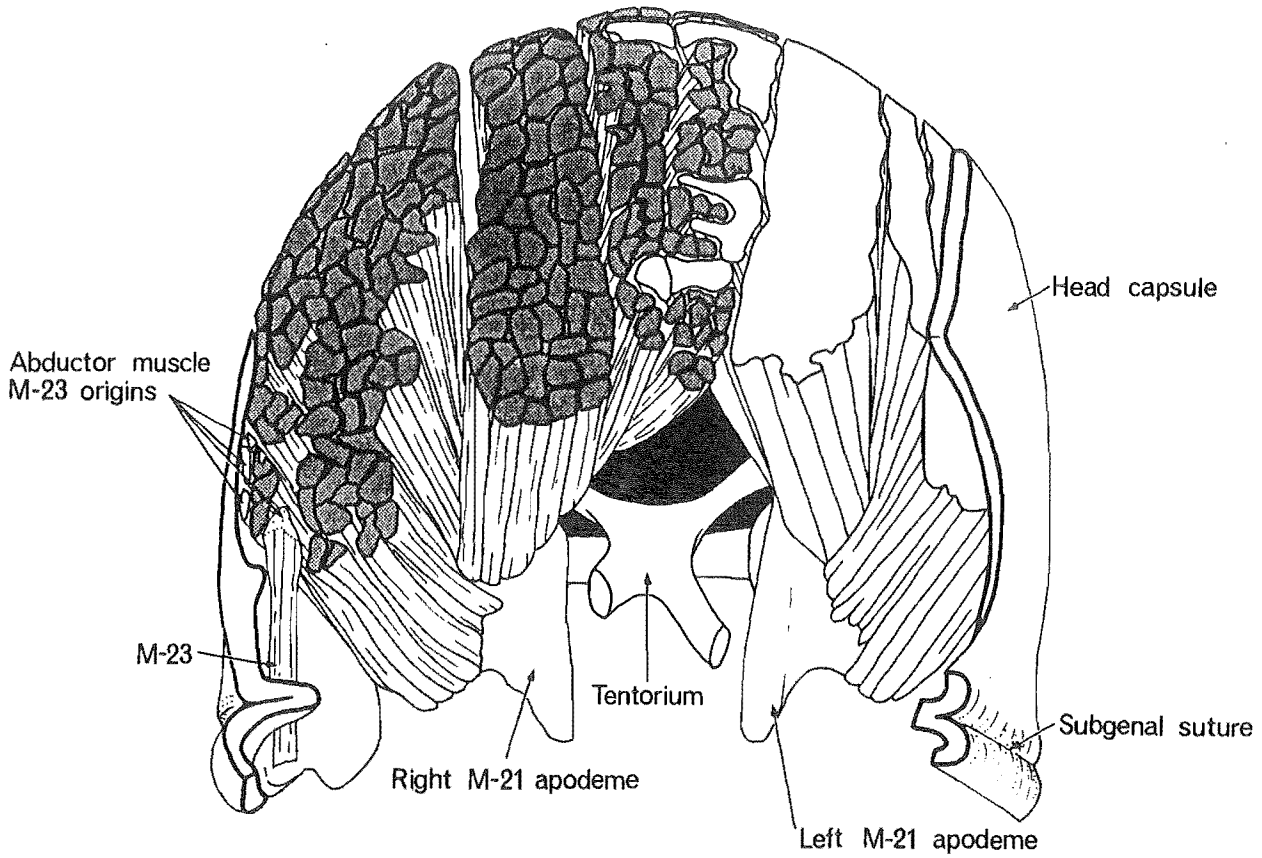
The principal adductor and abductor muscles of the weta.

(a) Frontal view of the head capsule with the epicranium partially removed to show the principal adductor muscles, M-21.

The origins of the right M-21 are toned, those of the left are not.

(b) Occipital view of the head capsule showing origins of muscles M-21 and M-23.

Lab.r. - labial retractor.


Head capsule
Abductor muscle
M-23 origins
M-23
Tentorium
Subgenal suture
Right M-21 apodeme
Left M-21 apodeme

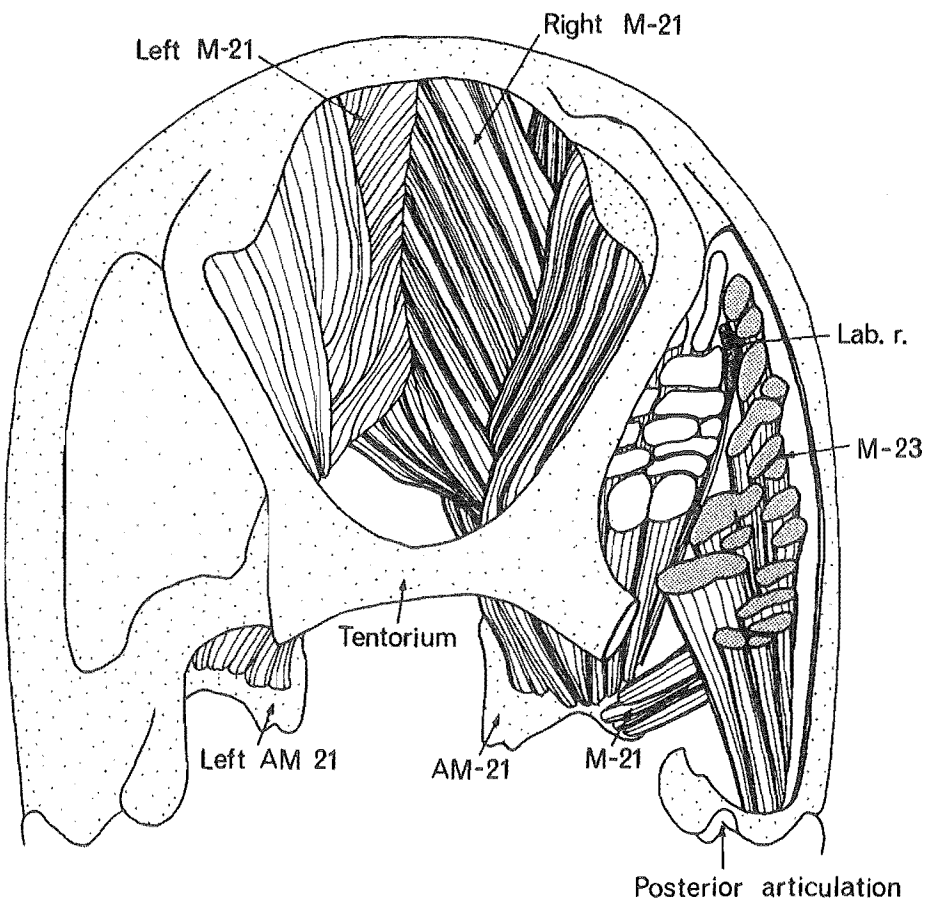

Left M-21
Right M-21
Lab. r.
M-23
Tentorium
Left AM 21
AM-21
M-21
Posterior articulation

Figure 13

The mandibular muscles of the weta, lateral and medial views.

(a) Lateral view. The M-21 origins are lightly toned. The M-23 (abductor) origins are darkly toned.

AM-23 - apodeme of muscle M-23.

M-23d - dorsal portion of muscle M-23.

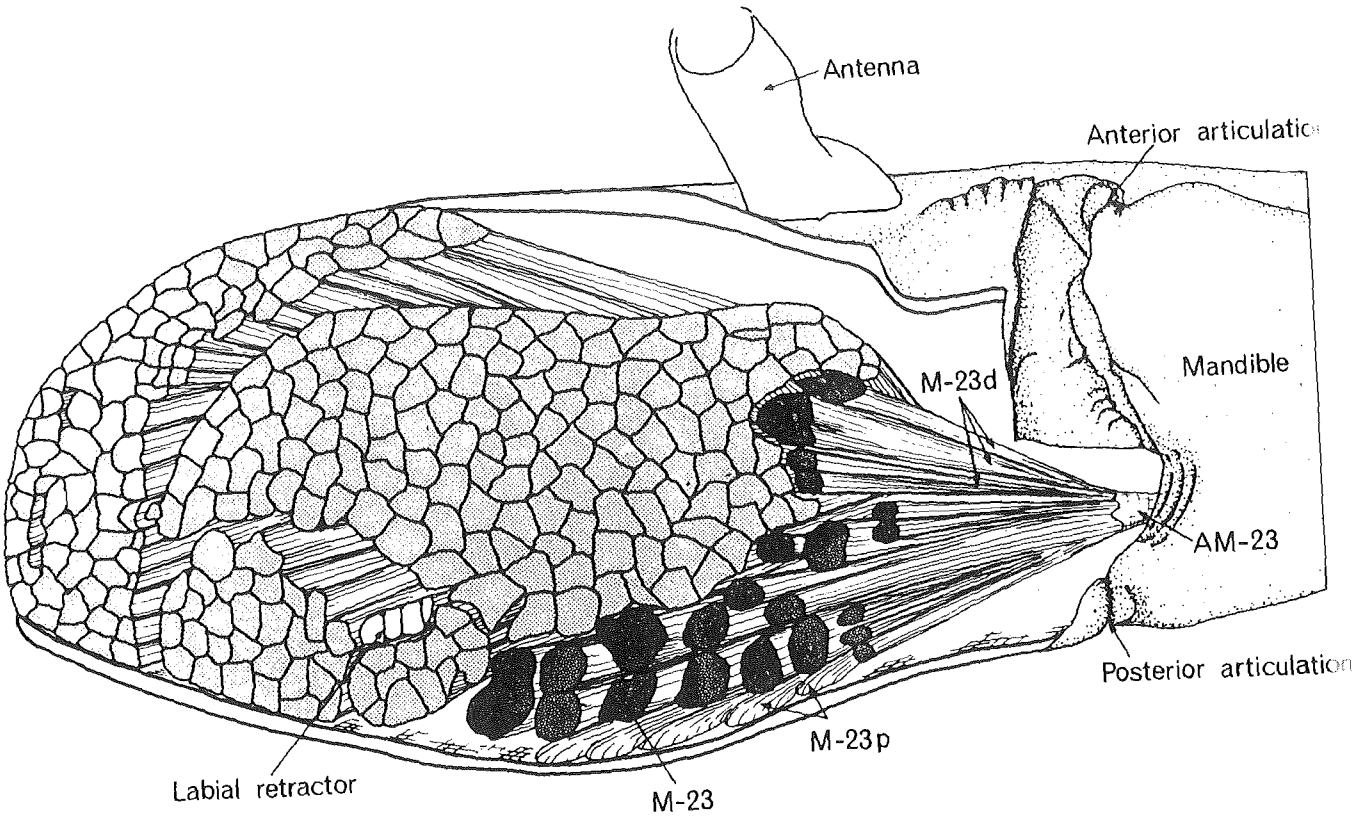
M-23p - abductor muscle bundles arising from the postgena.

(b) Medial view of the right mandible muscles.

C.O. - origin of muscle bundles showing a common apodeme with left M-23 bundles.

f - flexible region of the M-21 apodeme coupling it to the mandible.

i - spaces between muscle bundles normally filled by bundles from the left M-21.


Antenna
Anterior articulatio
Mandible
M-23d
AM-23
Posterior articulation
M-23p
Labial retractor
M-23

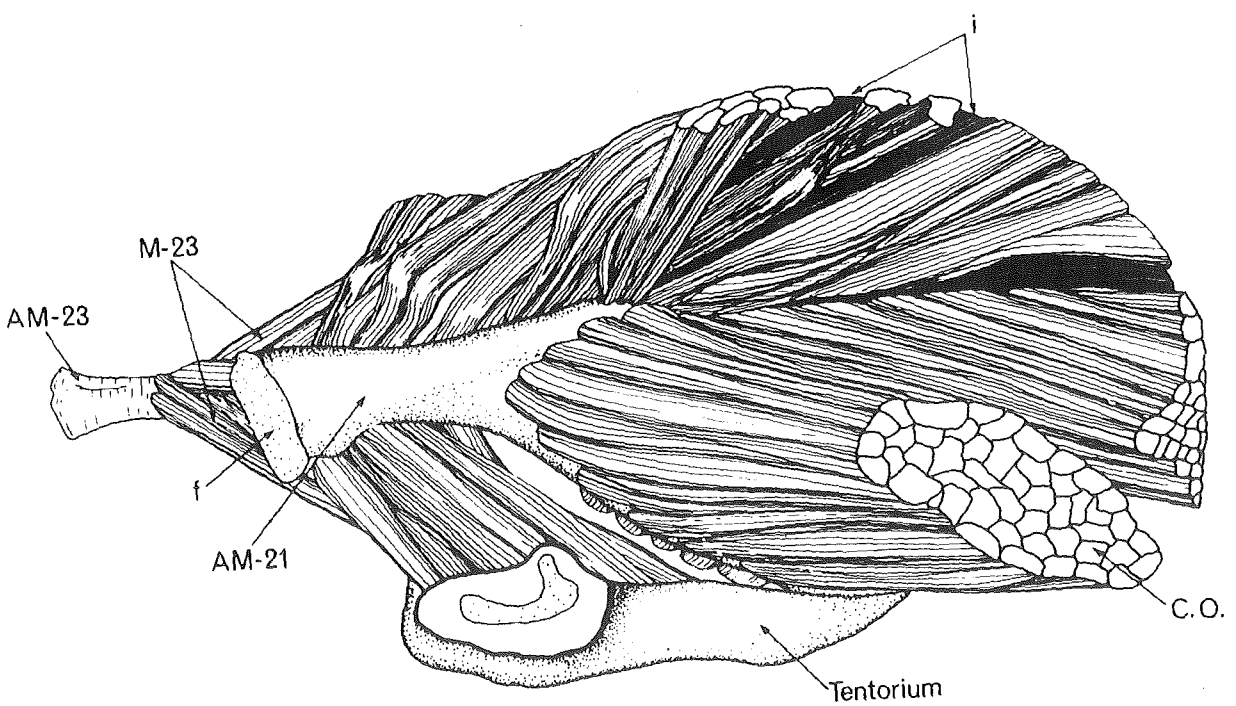
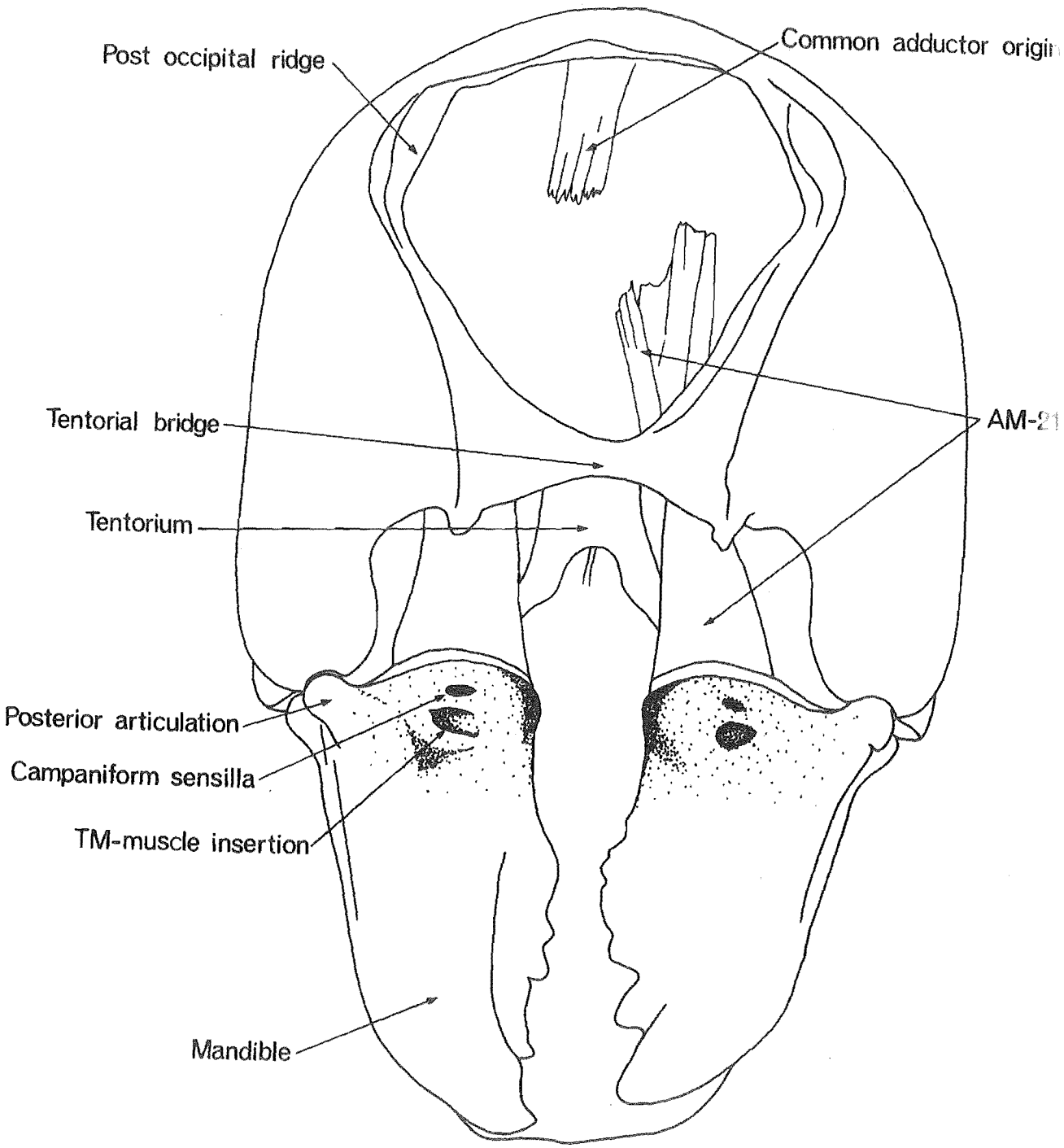

i
M-23
AM-23
f
AM-21
C.O.
Tentorium

Figure 14

Occipital view of the head capsule and mandibles of a female weta.

Drawn from a KOH-macerated preparation with the labium, hypopharynx, maxillae and all soft tissue removed.


Post occipital ridge
Common adductor origi
Tentorial bridge
AM-2
Tentorium
Posterior articulation
Campaniform sensilla
TM-muscle insertion
Mandible

of the midline (Figure 12a). This asymmetry was found in all animals.

The apodeme onto which all the muscle fibres insert is large and complex, receiving fibre bundles from many angles.

In the region between the muscle fibre insertions and the mandible it is heavily tanned and rigid. In this same region it alters shape from a compact cross-sectional area to a compressed sheet attaching obliquely to an extended area of the narrow mandible margin. There is a narrow zone of untanned, cuticle acting as a flexible coupling between the rigid body of the apodeme and the mandible (Figure 13b).

(2) Muscle 23 (M-23)

Muscle 23 is the sole abductor of the mandible. It lies in the most lateral part of the head capsule, its major component being in the angle between the gena and occiput with origins on both (Figures 12b, 13a). All these fibres insert on a thin flexible apodeme which attaches to a protuberance on the lateral basal margin of the mandible. Close to the mandible the apodeme branches to accommodate a fan-shaped group of muscle bundles arising more dorsally on the gena (Figure 13a). This group is much smaller than the rest of M-23.

(3) Muscle 26 (M-26)

M-26 is the only muscle lying largely within the cavity of the mandible. Its origin is on a long flexible apodeme attached to the hypopharynx. This passes through

Figure 15

Muscle 26, a hypopharyngeal retractor inserting on the lateral wall of the mandible.

The path of the M-26 motor neurones is shown by a heavy black line in nerve III, which it then leaves to run beneath muscle TM-2b for a short distance before diverging to the hypopharyngeal retractor.

Key to symbols: II, III - mandibular nerves leading to the suboesophageal ganglion; AM-21 - apodeme to muscle M-21; TM-1, 2a, 2b - tentoro-mandibular muscles.

The inset shows the region of the dissection.

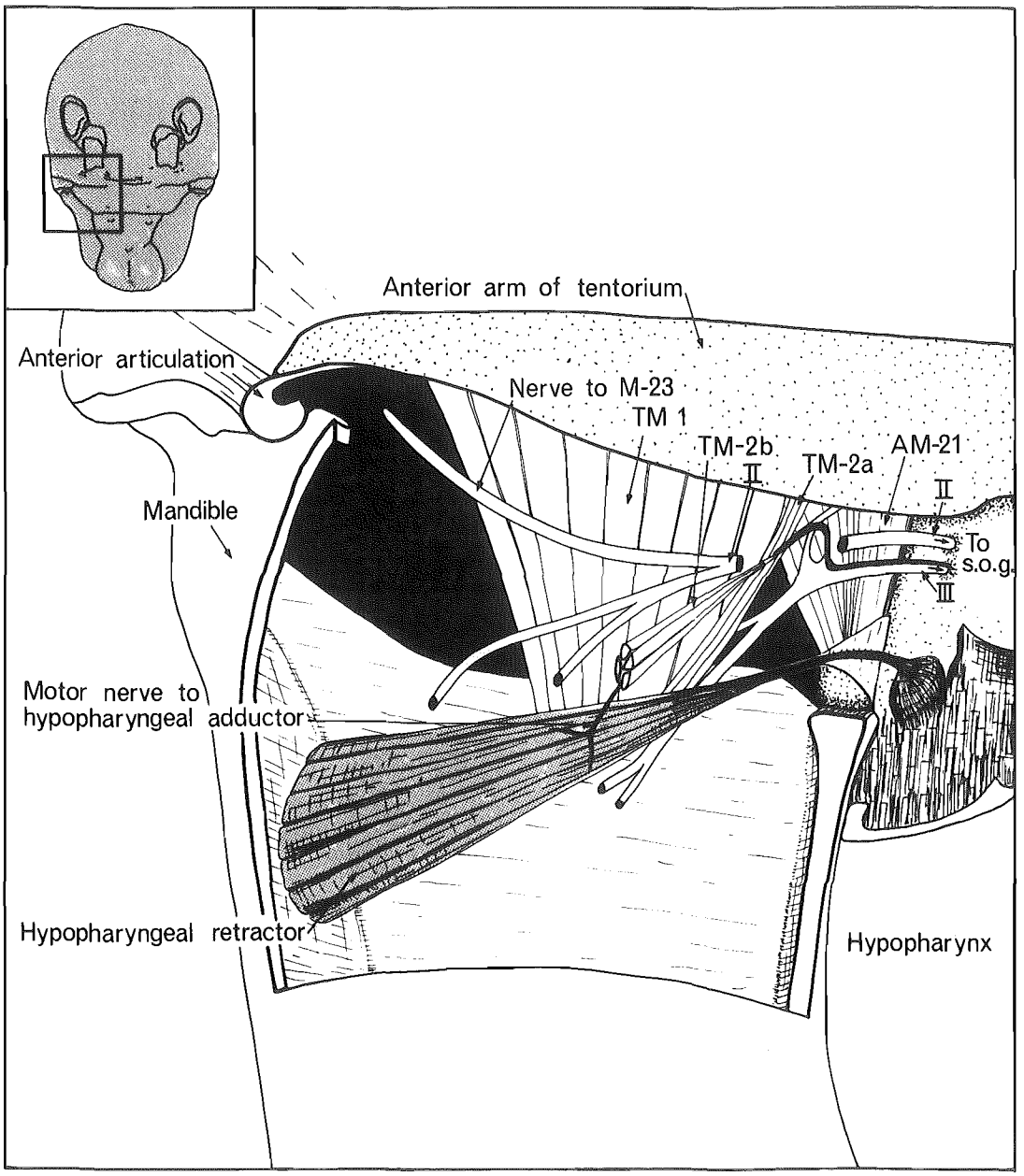

Anterior arm of tentorium
Anterior articulation
Nerve to M-23
TM 1
TM-2b
II
TM-2a
AM-21
II
Mandible
To
s.o.g.
III
Motor nerve to
hypopharyngeal adductor
Hypopharyngeal retractor
Hypopharynx

Figure 16

Projected view of the head showing the location of structures involved in mandibular functioning.

I,II,III - mandibular nerves from the sub-oesophageal ganglion.

AM-21 - apodeme of muscle M-21.

Ant.tent. - anterior arm of the tentorium.

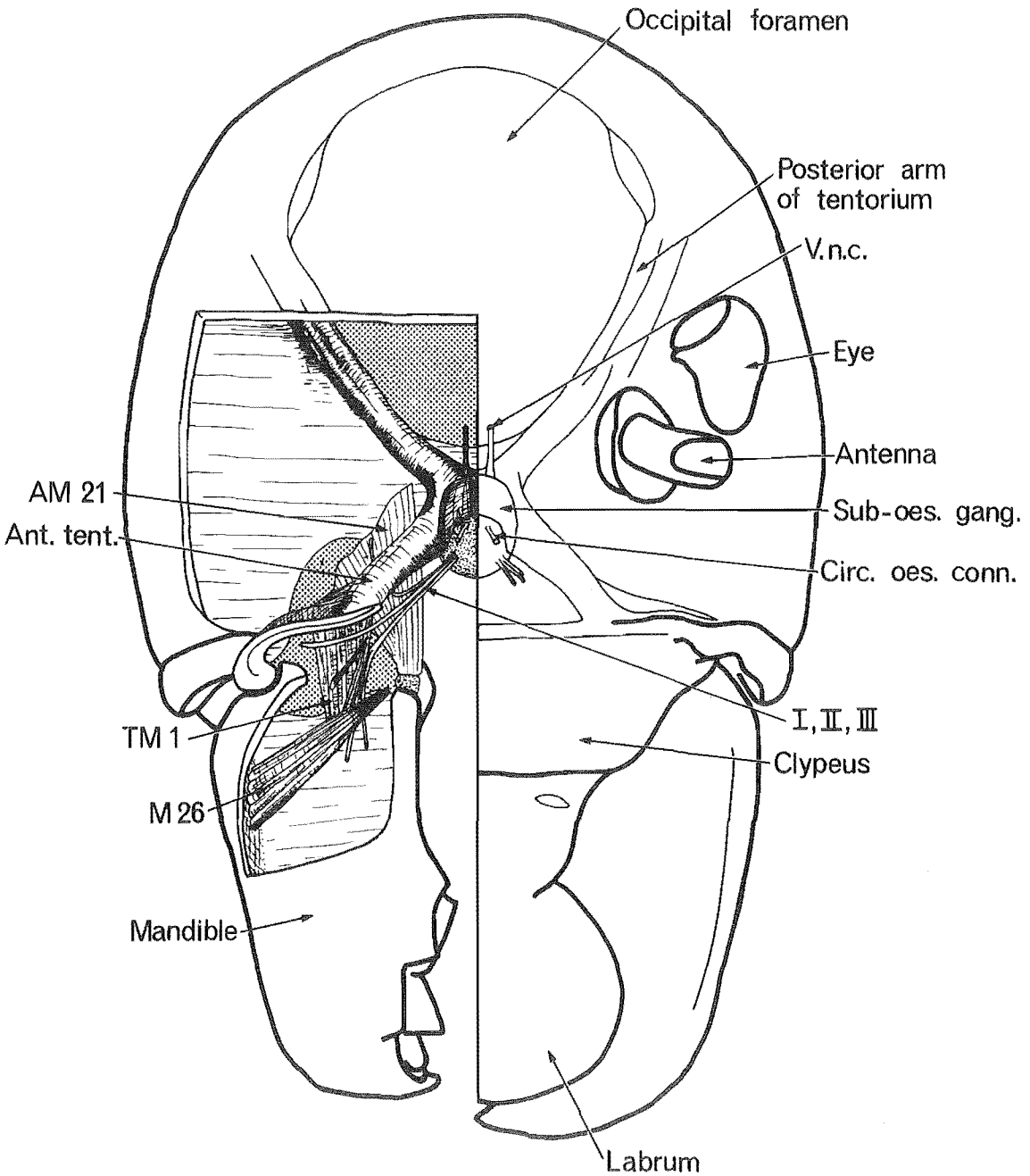
Circ.oes.conn. - circumoesophageal connectives.

M-26 - hypopharyngeal retractor muscle.

Sub-oes.gang. - suboesophageal ganglion.

TM-1 - tentoro-mandibular muscle.

V.n.c. - ventral nerve cord.


Occipital foramen
Posterior arm of tentorium
V.n.c.
Eye
Antenna
Sub-oes. gang.
Circ. oes. conn.
I, II, III
Clypeus
Labrum
AM 21
Ant. tent.
TM 1
M 26
Mandible

a sling of connective tissue at the inner angle of the mandible base which is also grooved just above the attachment site of the M-21 apodeme. The apodeme changes angle markedly at this point and a conical muscle mass arises from it and inserts onto the lateral wall of the mandible (Figure 15). The fibre bundles are very loosely associated at the insertion.

The two excitatory motor neurons leave the suboesophageal ganglion in nerve III and, together with the motor neuron for muscle TM-2b, they join the apodeme receptor strand (see Chapter VI) via the proximal process from the so-called "epipharyngeal ganglion (see Figure 17). The three axons leave the receptive strand and run beneath muscle TM-2b for a short distance before the two axons to M-26 branch off ventrally (Figure 15). Myography reveals two excitatory units, one continuously active at low levels of tension with the second being recruited at higher levels.

The function of M-26 is to retract the hypopharynx, although it is derived from a primary sternal adductor and is termed a hypopharyngeal adductor by many morphologists (Matsuda, 1965; Snodgrass, 1928). It is active in both feeding and the threat display, in which the hypopharynx is withdrawn.

(4) The tentoro-mandibular muscles

A group of small muscles arises on the anterior arm of the tentorium and inserts on two different parts of the basal region of the mandible. These appear to be homologous with one of the groups of primary sternal

adductor muscles which are present as small remnant muscles in many of the more primitive orthopterans. They correspond to muscle 25 in the nomenclature of Matsuda (1965). In order to distinguish between its various components, the group is referred to as the tentoro-mandibular muscles numbered TM-1, TM-2a and 2b and also includes the ventral muscle receptor organ (VMRO). The location of these is shown in Figure 16 and details of the components in Figure 17.

Muscle TM-1 is much the largest component of the muscle 25 group. It arises from the margin of the anterior arm of the tentorium (Figure 16) as a narrow elongate sheet approximately 1.5-2mm across and converges onto a raised cuticular process near the base of the mandible. The area of the elliptical insertion is approximately 0.95mm^2 in an adult male weta, showing that even the largest part of the TM grouping is only a small component of the total bulk of adductor muscle.

The TM-1 muscle runs obliquely across the joint between the head capsule and the mandible, its long axis lying at an angle of approximately 50^{o} to the plane of opening with the mandible in the rest position. The angle decreases as the mandible opens.

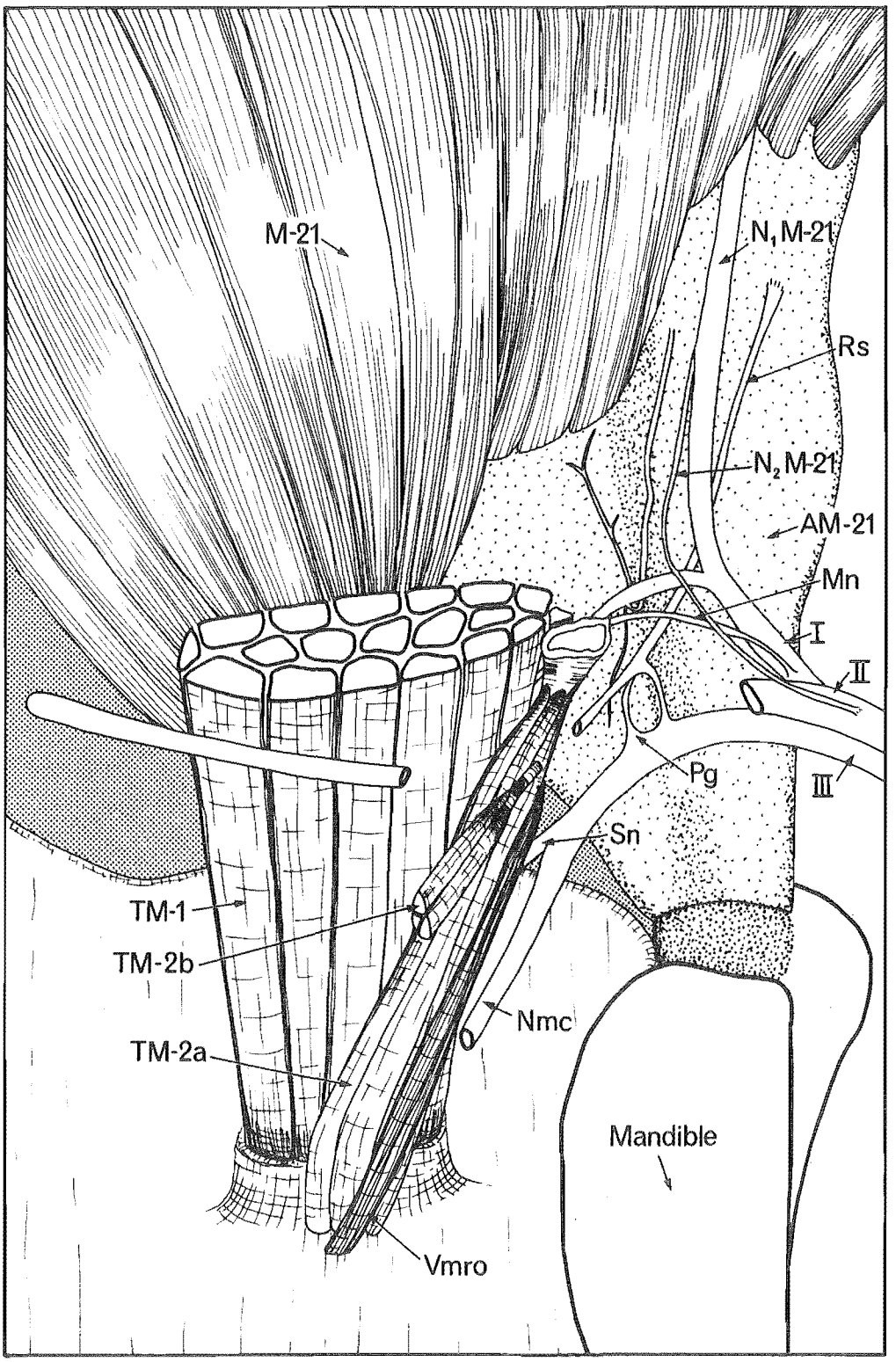
Mean sarcomere lengths from 8.3-13.0μm were obtained from counting at least 10 sarcomeres per fibre in more than 30 fibres taken from different regions of the muscle in different preparations. The muscle was fixed in situ in alcoholic Bouin's.

Muscle TM-2a arises from the tentorium on the medial margin of TM-1. Usually the origin is a short

Figure 17

The tentoro-mandibular musculature and associated nerves as revealed by frontal dissection.

Am-21 - apodeme of muscle M-21; Mn - motor nerve to TM-1, TM-2a and the VMRO; N_1M-21 - major motor nerve to muscle M-21; N_2M-21 - small nerve from trunk II also supplying muscle M-21; Nmc - nerve to the cusps and more distal parts of the mandible; Pg - group of cell bodies supplying the apodeme strand receptor; Rs - receptor strand of the apodeme strand receptor; Sn - sensory nerve from the VMRO; VMRO - ventral muscle receptor organ; I, II, III - major mandibular nerve trunks running from the suboesophageal ganglion.


M-21
N₁M-21
Rs
N₂M-21
AM-21
Mn
I
II
III
Pg
Sn
TM-1
TM-2b
TM-2a
Nmc
Mandible
Vmro

apodeme (Figure 17) but this may be contained within the muscle fibres which then appear to arise directly from the tentorium. TM-2a is a flattish strip of muscle which runs obliquely over the frontal or anterior surface of TM-1 and inserts onto the mandibular cuticle immediately adjacent to the raised cuticular process bearing the TM-1 insertion. Muscle TM-2a broadens and deflects slightly as it passes over this process. In one animal TM-2a was found to bifurcate after the usual origin and the two approximately equal portions inserted in different sites beside the TM-1 insertion.

Muscle TM-2b arises from TM-2a a short distance from the tentorium. In some animals a distinct apodeme was visible as illustrated in Figures 17 and 32, but in others the fibres of the two muscles appeared to intermingle and those of TM-2b ran up towards the tentorium. TM-2b is a smaller muscle than TM-2a and unlike TM-1 and TM-2a it inserts on the frontal or anterior surface of the mandible about 2mm from its basal margin. Therefore it is approximately 2.5mm long when the mandibles are closed and it lies at an angle of about 45^{o} to TM-2a. When sectioned and stained with Mallory's Triple Stain it differed in appearance from TM-2a, and the sarcomeres were shorter. A count of 10 different values from lengths of TM-2b fibre each spanning at least 10 sarcomeres gave mean lengths in the range 4.1-6.2μm in one preparation where TM-2a ranged from 5.4-11.6μm. Another preparation gave values of 4.3-5.7μm (TM-2b) and 8.2-13.6μm (TM-2a).

Muscle TM_2b is part of the dorsal muscle receptor

organ which is described more fully in Chapter V.

The ventral muscle receptor organ (VMRO) is the fourth component of the tentoro-mandibular complex. It is found on the medial margin of the group lying almost parallel to muscle TM-2a, but spiralling round it by approximately 180°. Its origin and insertion are close to those of muscle TM_2a, but the two structures are not linked in any other way. Its location is shown in Figure 17. A more detailed description of its anatomy is given in Chapter VI.

III NEUROANATOMY

All the sense organs and muscles of the mandibles are innervated by nerves from the suboesophageal ganglion (SOG). This ovoid structure is situated partially under the body of the tentorium (Figures 16, 18) and all the mandibular nerves leave from its dorsal surface just anterior to the circumoesophageal connectives. The position of the suboesophageal ganglion within the head, its relation to the supraoesophageal ganglion and the major nerves to the other mouthparts are shown in Figures 18 and 19.

Four nerves leave the SOG in the group that supplies the mandible. Three of these are large and are termed nerve trunks I, II and III. The fourth (IV) is a much smaller nerve which innervates the basal region of the hypopharynx (Figure 19b). Between nerve trunk IV and the hypopharyngeal nerve, which innervates the more distal parts of the hypopharynx, is a small web of tissue

which extends dorsally as a fine strand which attaches to the labral nerve from the supraoesophageal ganglion. The strand is attached to nerve IV at one point (Figure 19b). Under the dissecting microscope it did not resemble neural tissue.

The other three nerves extend dorsally before passing over the M-21 apodeme. At this level they begin to branch, supplying both sense organs and muscles. Where they pass over the apodeme the nerves are partially obscured by the anterior arm of the tentorium, trunk I being totally obscured. All three mandibular nerves contain both sensory and motor axons. Nerve I has sensory branches to the basal group of mandibular campaniform sensilla and to the M-21 apodeme. These are described in more detail in Chapter VI. The major branch of nerve I passes into muscle M-21 as nerve (N1 M-21), (Figure 17). In transverse section it shows 18 large profiles. Back-filling this nerve with cobalt chloride has revealed 18 cell bodies in the dorsal region of the suboesophageal ganglion close to the entry of the mandibular nerves. A second, much smaller nerve, N2 M-21, also passes into the principal adductor muscle after leaving trunk II (Figure 17).

The motor neurones to muscles TM-1, TM-2a and the VMRO are carried in the same fine branch from nerve I. The nerve passes behind the TM muscles, as seen in frontal dissection (Figure 17) and branches just before it reaches TM-1. Muscle TM-2b is innervated by a single motor neurone which runs in trunk III before passing into the apodeme receptor strand and thence to TM-2b

Figure 18

A parasagittal section of the head of an adult male weta, showing the positions of the major nerve ganglia in relation to other structures in the head.

Ant. - antenna; Br. - supraoesophageal ganglion ("brain"); C.c. - corpus cardiacum; c.o.c. - circum-oesophageal commissure; Fr.g. - frontal ganglion; Hyp. - hypopharynx; Lab. - labium; Lab.n. - labial nerve; Lbr. - labrum; L.p. - labial palp; Max. - maxilla; Md. - mandible; M.g. - muscles suspending the gut; M.hyp. - retractor muscles of the hypopharynx arising from the posterior arm of the tentorium; M.lab. - retractor muscles of the labium arising from the posterior arm of the tentorium; M-21 - adductor muscle M-21; N.hyp. - hypopharyngeal nerve; N.max. - nerves to the maxillae; N.md. - nerves to the mandible; N.t-th - nerve supplying the tentoro-thoracic muscles; Oes. - oesophagus; Op.n. - optic nerve; Ph. - pharynx; S.o.g. - suboesophageal ganglion; Tent. - tentorium; T-th. - muscles attached to the tentorium and passing into the thorax; V.c.n. - ventral nerve cord.

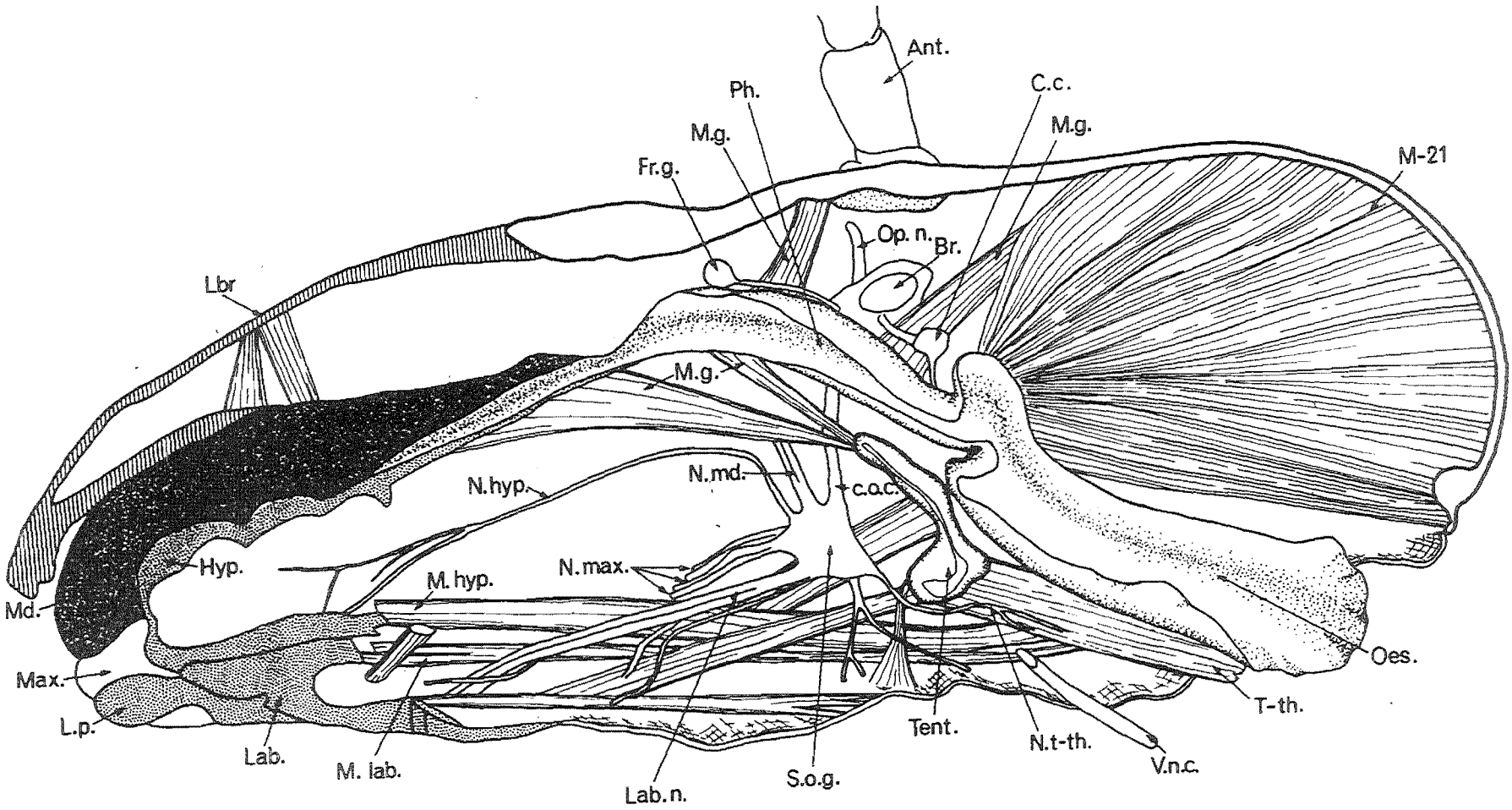

Ant.
Ph.
C.c.
M.g.
M.g.
Fr.g.
M-21
Op. n.
Br.
Lbr
M.g.
N.hyp.
N.md.
c.o.c.
Hyp.
M. hyp.
N.max.
Md.
Max.
L.p.
Lab.
M. lab.
Lab.n.
S.o.g.
Tent.
N.t-th.
V.n.c.
T-th.
Oes.

Figure 19a

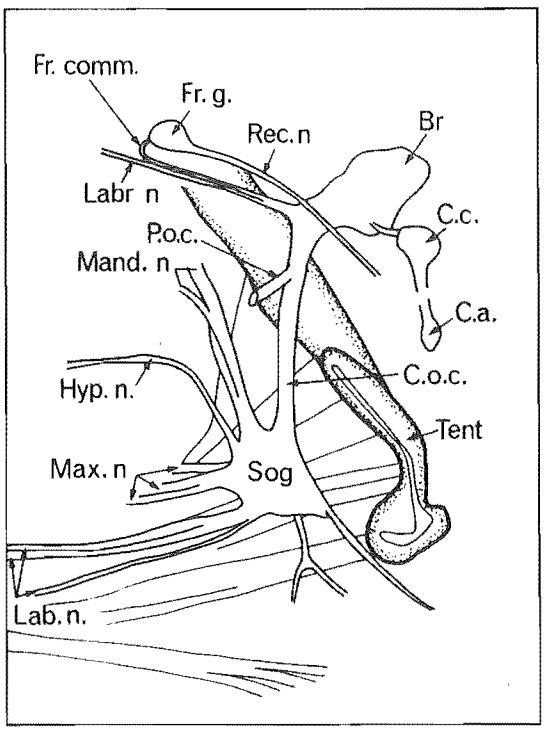
The neural ganglia of the head of Hemideina and their principal nerves.

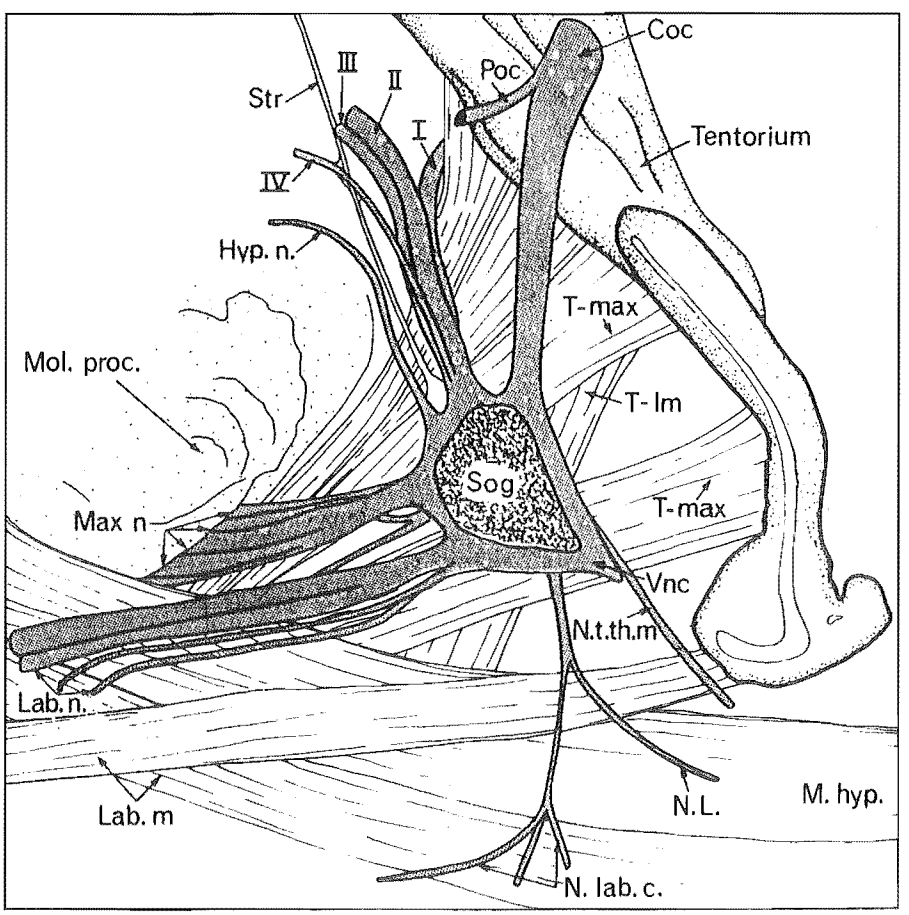
Br. - supraoesophageal ganglion; C.a. - corpus allatum; C.c. - corpus cardiacum; C.o.c. - circum-oesophageal commissure; Fr.comm. - frontal commissure; Fr.g. - frontal ganglion; Hyp.n. - hypopharyngeal nerve; Lab.n. - labial nerves; Labr.n. - labral nerves; Mand.n. - mandibular nerves; Max.n. - maxillary nerves; Poc. - post-oesophageal commissure; Rec.n. - recurrent nerve; Sog - suboesophageal ganglion; Tent. - tentorium.

Figure 19b

The suboesophageal ganglion of Hemideina, its major nerves and surrounding structures.

I, II, III - the mandibular nerves; IV - nerve leaving the SOG with the mandibular nerves, but innervating the hypopharynx; Coc. - circumoesophageal commissure; Hyp.n. - hypopharyngeal nerve; Lab.m. - retractor muscle of the labium; Lab.n. - labial nerve; M.hyp. - retractor muscle of the hypopharynx; Max.n. - maxillary nerves; Mol.proc. - molariform process of the mandible, showing through the wall of the hypopharynx; N.L. - sensory nerve passing into the neck region; N.lab.c. - nerve innervating the cuticle at the base of the labium; N.t.th.m. - nerve to the tentoro-thoracic musculature; Poc. - postoesophageal commissure; Str. - strand running from the SOG to the labral nerve and joined to nerve IV; Sog. - suboesophageal ganglion; T-lm - muscle between the tentorium and the labium; T-max - muscle between the tentorium and the maxilla.


Fr. comm.
Fr. g.
Rec. n
Br
Labr n
C.c.
P.o.c.
Mand. n
C.a.
C.o.c.
Hyp. n.
Tent
Max. n
Sog
Lab. n.


Coc
III
II
Poc
Str
I
Tentorium
IV
Hyp. n.
T-max
Mol. proc.
T-lm
Sog
T-max
Max n
Vnc
N.t.th.m
Lab. n.
N.L.
M. hyp.
Lab. m
N. lab. c.

near its origin. The motor innervation of the muscle receptor organs is described more fully in the section on sense organs (Chapter VI). The two motor neurones to the hypopharyngeal retractor, M-26, follow the same path as that to TM-2b, before branching off to M-26 a short distance from the origin of TM-2b (Figure 15).

The motor neurones to muscle M-23, the abductor, are carried in nerve trunk II, which passes in front of the TM muscles (Figure 15). Seven large profiles were seen in sections of this nerve, and up to six cell bodies have been found in a single cobalt backfill, indicating at least six motor neurones. Nerve II supplies cuticular sense organs in the basal region of the mandible, particularly on the frontal surfaces and near to the anterior articulation. These are discussed in more detail in Chapter VI and illustrated in Figure 32. One small branch from nerve II passes into muscle M-21 (nerve N2 M-21, Figure 17) but its sensory or motor function has not been determined.

The principal components of nerve III are sensory axons from the apodeme strand receptor, the ventral muscle receptor organ and the more distal parts of the mandibular cuticle, including the cusps. These are described more fully in Chapter VI.

IV MECHANICAL FUNCTIONING

The mandible is a simple unjointed appendage with its movements largely confined to a single plane by the existence of two articulations. Its functioning

presents two principal mechanical requirements. It must achieve the wide gape seen in the threat display and also the strong closure in defensive biting. In addition the mandible movement must be restricted to one plane in both abduction and adduction, particularly during strong isometric contractions when the two mandibles meet.

(1) Stability

Stability of the mandible is conferred largely by the triangular shape of the mandible base, with the two articulations and the M-21 apodeme insertion placed at the three angles (Figure 20). The articulations alone do not restrict the mandible to a single plane of movement. The anterior articulation dislocates readily in a relaxed animal. Contraction of any of the muscles, disregarding the hypopharyngeal retractor, tends to rotate the mandible about the ball-and-socket posterior articulation, forcing the mandible into contact with the head capsule at the anterior articulation.

(2) Plane of movement

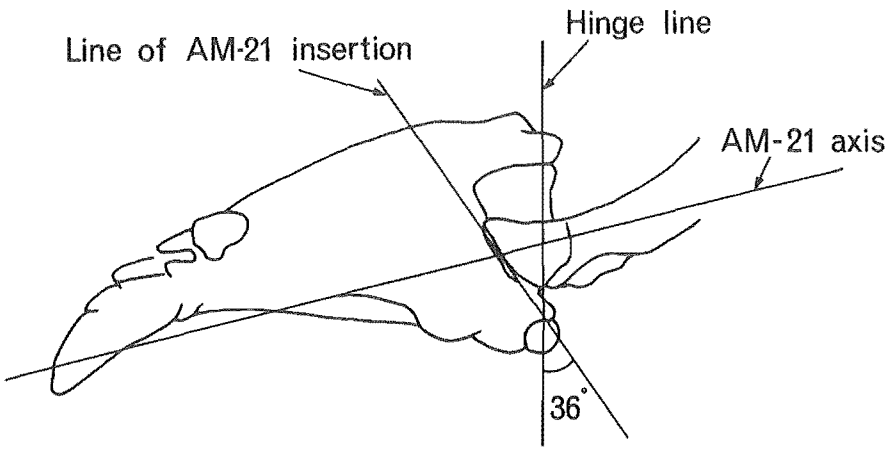
The two mandibles do not move in exactly the same plane. The posterior articulations are displaced further from the midline than the anterior articulations, measured with the head capsule viewed as in Figure 8. With the head oriented long axis horizontal, the mandibles were raised slightly out of the viewing plane when opened, and closed downwards as well as towards the midline. The angle by which each mandible departed

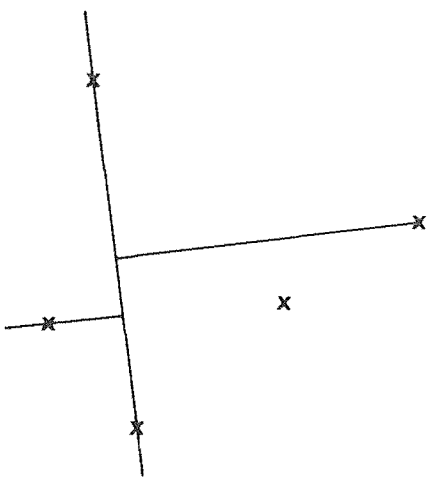
Figure 20

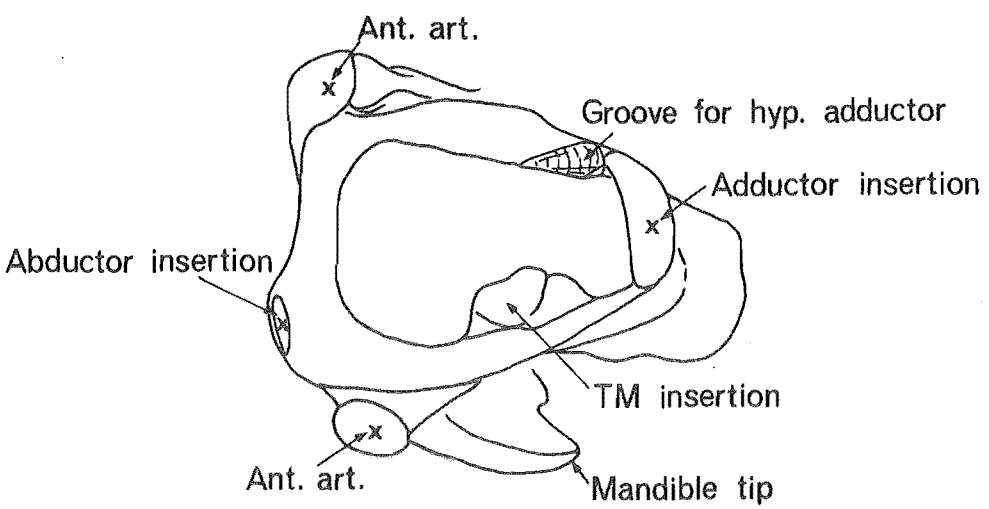
The mechanics of the mandible.

The upper diagram shows a medial view of a right mandible, illustrating the relationship of the apodeme of adductor muscle M-21 to the hinge line.

The lower diagram is a view into the body of the mandible from the basal end to indicate the relationships of the muscle insertions to the articulations. The displacements from the line between the articulations (the hinge line) are indicated in the line diagram immediately above.


Line of AM-21 insertion
Hinge line
AM-21 axis
36°




Ant. art.
Groove for hyp. adductor
Adductor insertion
Abductor insertion
TM insertion
Ant. art.
Mandible tip

from the horizontal plane varied from -1^{o} to 7^{o} in different specimens. Similar values were recorded for the two mandibles in any one animal, the combined deviation from a single plane of action varying from 1^{o} to 14^{o}. In other words, the angle between the planes of movement of the two mandibles varied from 179^{o} to 166^{o}.

(3) Joint angle

Although the gape of a threatening weta appears large, up to 13mm in a large male of 26mm head length, the angle of opening is not extreme. Much of the gape derives from the wide separation of the two hinge lines. During induced threatening in restrained adult males, the maximum recorded value was 45^{o} open from rest in each mandible. The means were $\bar{x} = 38^{o}$ in the right, $\bar{x} = 36^{o}$ in the left ($n = 15$). The angle for the left exceeded that for the right in only three of the fifteen animals. In addition, full closure continued approximately 5^{o} past the rest position in the right mandible. The maximum angle of action was therefore approximately 50^{o}.

The mechanical requirements of a wide gape are in conflict with achieving a strong bite. Many arthropods have adductor muscles inserted far into the body of the mandible to achieve a maximal mechanical advantage (examples in Manton, 1964). To achieve a wide gape in such a situation would require great elongation of the adductor muscles.

(4) Muscle TM-1

Only the TM muscles pass into the body of the

mandible and even these insert close to the base. Their length change on full opening is further reduced by two factors. A smaller mechanical advantage, in comparison to M-21 (Figure 20) requires a smaller length change. Secondly, the axis of muscle TM-1 lies at an angle of 50^{o} to the plane of opening when the mandible is in the rest position. This orientation requires a smaller percentage change in length during opening than if the axis of the muscle lay in the plane of opening.

The contribution of TM-1 to the total force of adduction is small. The cross sectional area of its insertion was measured at $0.92mm^{2}$. Using a value of $3kg.cm^{-2}$ for the force of muscle contraction (Hoyle, 1972, reports values of $1.6kg.cm^{-2}$) and by measuring its line of action and mechanical advantage, a closure torque of 4.0gm.cm was estimated, an insignificant amount compared to the values in excess of 1200gm.cm routinely recorded (see below).

(5) Muscle M-21

The principal adductor, M-21, inserts via its apodeme on to the innermost margin of the mandible base, approximately 4mm from the articulations. It thus operates at a 1/2.6 mechanical advantage, calculated using the full length of the mandible. The advantage is 1/1.6 calculated at the proximal cusps performing the molar functions.

The M-21 apodeme axis is approximately in parallel with the long axis of the mandible, neither being at right angles to the hinge line, the axis formed by the

two articulations (Figure 20). The rigid apodeme attaches obliquely onto the mandible margin. This configuration may be to increase the coupling area to reduce the load per unit area on the flexible cuticle linking the mandible to the apodeme.

The wide displacement of the M-21 apodeme insertion from the midline may be more than 4mm in a large weta. During a full mandibular excursion of 50^{o} the apodeme is displaced more than 3.3mm in the direction of its long axis, together with a smaller amount of lateral displacement. This requires that some of the muscle fibres arising on the vertex must approximately double their length during wide gaping. Owing to the multi-pennate nature of the muscle not all fibres will be elongated by such a high percentage of their length.

The maximum strength of bite recorded was 1900gm.cm, equivalent to a force of more than 4kg applied at the M-21 apodeme insertion. This was obtained in a unilateral bite with a surgical silk coupling from the transducer to the mandible. Bites routinely reached values between 1100-1300gm.cm. in the experiments described in Chapter VII, where solid couplings were used. The higher value under these conditions may have resulted from altered afference due to the slightly elastic coupling allowing some closure movement, or from differences in cusp contact afference caused by the more flexible coupling. While the bite strength was seldom exactly equal in the left and right mandibles, recorded independently at different times, neither mandible proved consistently stronger.

(6) Muscle M-23

The sole abductor muscle (M-23) works at a mechanical advantage of approximately 1/12. Opening torques up to 50gm.cm. were recorded from two preparations.

(7) The head capsule

During the strongest defensive biting the head capsule distorted visibly. Despite the thickening and tanning of the frontoclypeal region between the two anterior articulations, the head capsule spread laterally in the region of the hinge lines. The remainder of the head capsule flattened perceptibly at the same time.

V MYOGRAPHY

By recording myograms during feeding, induced defensive biting and spontaneous biting against the force transducer it was found that the weakest movements were mediated by the tentoro-mandibular muscles. The M-21 muscle bundles arising near to the midline of the head were recruited next, with the more laterally disposed bundles discharging on the strongest movements. Myograms were recorded from 12 preparations.

(1) Muscle TM-1

Figure 21a shows muscle TM-1 active in a weak spontaneous bite from a maintained open position. Little activity was found in the ipsilateral M-21 traces. There was reduced TM-1 activity in the subsequent

induced defensive bite where the much greater force was from a high level of M-21 activity. As some bundles of M-21 do not have an origin on the external cuticle they were not ever recorded from. Nor were bundles arising on the post gena. It cannot therefore be stated with certainty that only muscle TM-1 was active in the weakest movements, but all the recordings were consistent with such a conclusion. TM-1 was almost continuously active in all preparations (e.g. Figure 22a). Activity ceased only during voluntary opening and even then low levels of discharge were recorded at the initiation and termination of opening. In Figure 22d there is little activity in the TM-1 trace prior to the defensive bite. This recording was made after cutting the sensory nerve from the VMRO, a procedure that also required more extensive dissection. In several preparations cutting the VMRO sensory nerve appeared to reduce TM-1 activity. The dependence of TM-1 activity on sensory input was not pursued. All TM-1 myograms were obtained from a partially dissected preparation (see Chapter II) which may have resulted in an increased level of central excitation and elevation of motor discharge.

Reflexive excitation of TM-1 by imposed mandibular opening is clearly shown in Figure 22b. Unlike for muscle 21, resistance reflexes to whole mandible movement were recorded from TM-1 in all preparations.

(2) Muscle M-21

(a) Resistance reflexes. Resistance reflexes in response to whole mandible opening were not readily

recorded from M-21, unless the movement was superimposed on voluntary closure. Figure 23a shows activity from three different sites in the left M-21 in response to rapid displacement of the left mandible by a hand-held probe. While not monitored, the very rapid rate of opening was certainly in excess of the rates observed in spontaneous opening. In this preparation, opening rates comparable to those produced voluntarily elicited no response.

Bilateral responses to unilateral stimulation were recorded from two preparations. Imposed opening of the left mandible, applied with a surgical silk loop over the cusp region elicited responses from frontal sites of both left and right M-21 (Figure 23b). The effect was not completely symmetrical. Right mandible stimulation elicited much stronger ipsilateral responses, although weak responses were recorded from the left M-21. Stimulation of the left mandible gave comparable responses in both animals (Figure 23c).

(b) Voluntary activity. Maintained mandibular opening did not elicit a tonic discharge from M-21 in an unstimulated animal, although weak closure movements were frequently observed. However, within a sequence of defensive bites a low level of activity was often sustained, resulting in a small but measurable level of tension (Figure 21c). This residual tension level was found in all preparations where repeated defensive biting was induced, and complicated the determination of bite onset (Chapter VII). Low levels of tonic discharge continued during the relaxation following

some powerful bites, but not all (compare Figure 21b and Figure 22c).

Defensive bites could still be induced following section of the sensory nerve from the VMRO (Figure 22d). In this recording, high frequencies of discharge occurred in all ipsilateral traces, including TM-1. The irregularities in the bite force were probably attributable to the frontal dissection necessary to section the nerve.

Figure 21d shows myograms from two different recording sites in the left M-21 during a feeding sequence. The trace from the medial site shows earlier recruitment than the more lateral bundle, with longer bursts at a higher frequency. This shows the typical pattern of recruitment. In weaker chewing the more lateral sites often showed intermittent activity, whereas the more medial groups were invariably active. Feeding sequences lacking M-21 activity were not recorded.

Figure 21

Adductor muscle myogram recordings.

(a) Myograms recorded during a weak voluntary bite of the right mandible only. The lower four traces are myogram recordings.

[i] Force transducer, closure is a downwards deflection. Calibration 350gm.cm.

[ii] M-21 of the left mandible.

[iii-iv] M-21 of the right mandible.

[v] TM-1 of the right mandible.

(b) Myograms recorded during unilateral induced defensive bite. The traces are as in part (a). Force transducer calibration 350gm.cm.

(c) Myograms from a medial-frontal site in M-21 of the right mandible.

[i] Recording while quiescent.

[ii] During spontaneous biting in the right mandible.

[iii] Superimposed force transducer traces taken during [i] and [ii] above. Down denotes closure. Vertical calibration 900gm.cm.

(d) Myograms from M-21 of the left mandible during apple chewing. The lower pair of traces is a continuation of the same sequence as the upper pair.

Traces [i,iii] from a fronto-lateral site beside the eye; [ii,iv] from a fronto-medial site close to the midline. Calibration: 1 second.

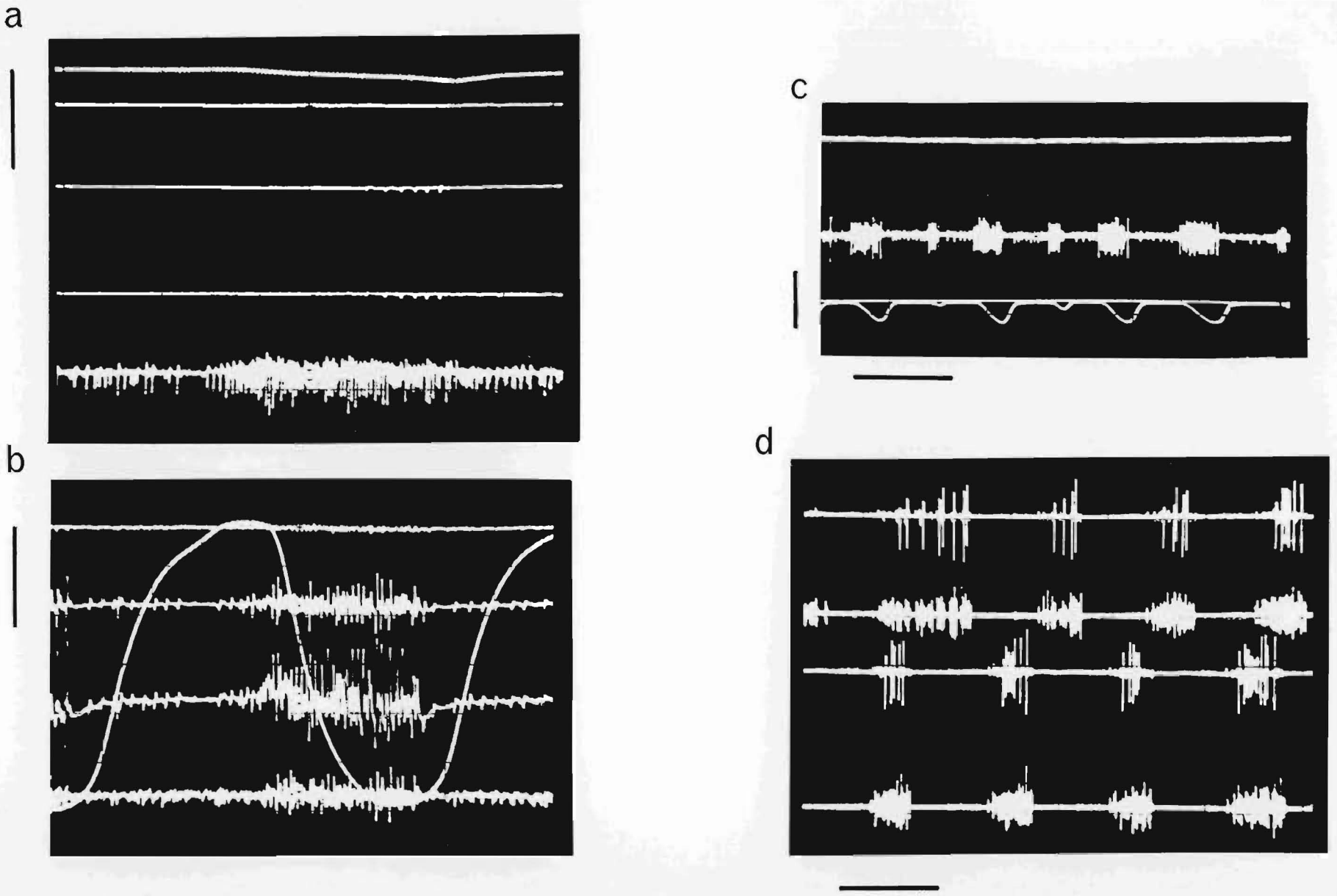

a
b
c
d

Figure 22

Myograms from different muscle groups during imposed oscillation of the right mandible.

(a) From the tentoro-mandible (TM-1) muscle in the rest position showing the spontaneous activity in the absence of stimulation.

(b) Recording from the TM-1 muscle during imposed oscillation of the right mandible.

In (a) and (b) the arrows indicate the direction of closure. The time marker is one second.

(c) Myogram activity during a unilateral left induced defensive bite.

Trace [i] Force transducer output. Downwards deflection indicates increasing force. Vertical calibration: 720gm.cm.

[ii] Right M-21 activity.

[iii-v] Activity from three different sites in the left M-21.

Horizontal calibration: 0.5 seconds.

(d) Myogram activity during a unilateral left induced defensive bite following left VMRO nerve section.

Trace [i] Force transducer output, as in (c). Vertical calibration 360gm.cm.

[ii-iv] As in (c) above.

[v] Activity in the left TM-1. Horizontal calibration 1 second.

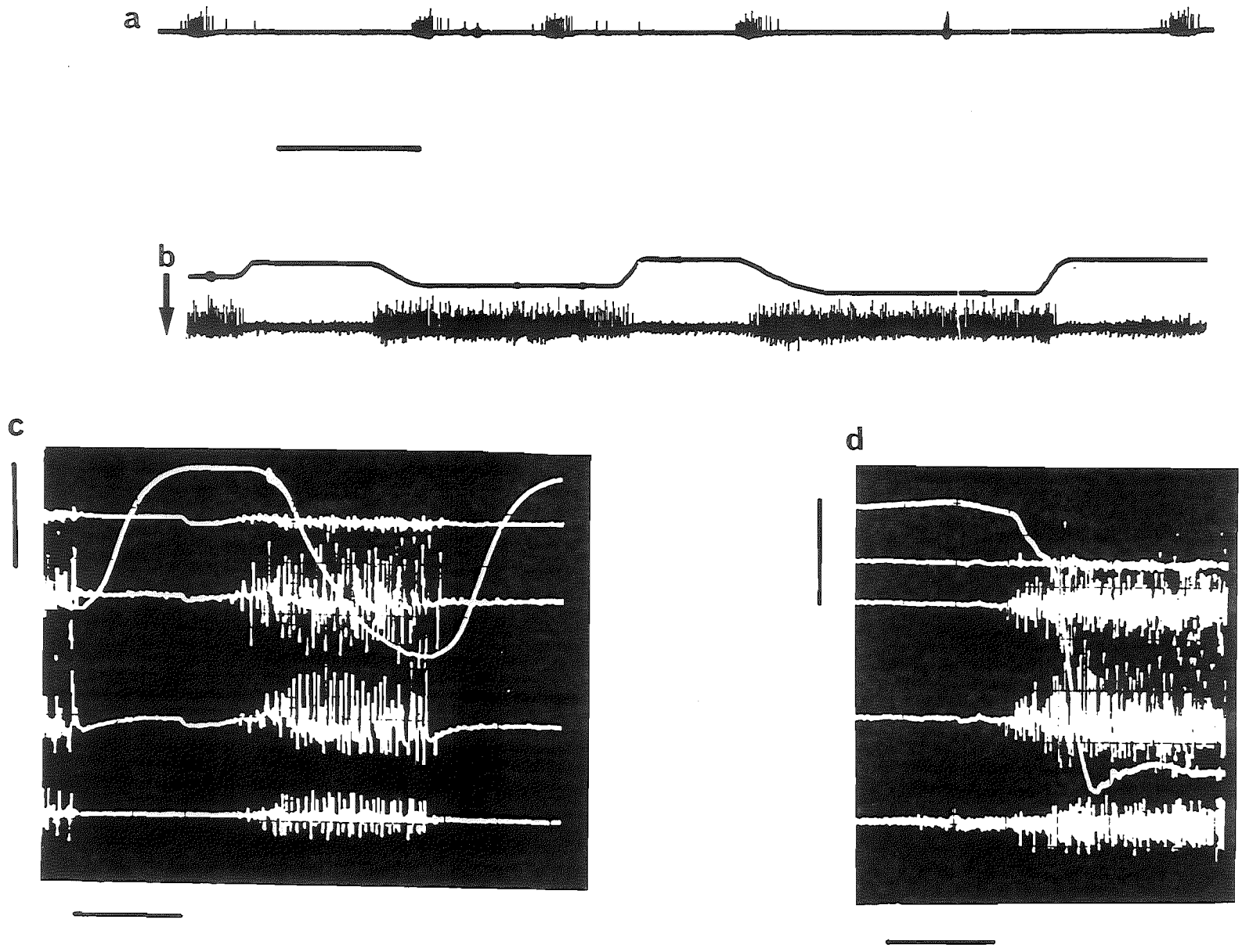

a
b
c
d

Figure 23

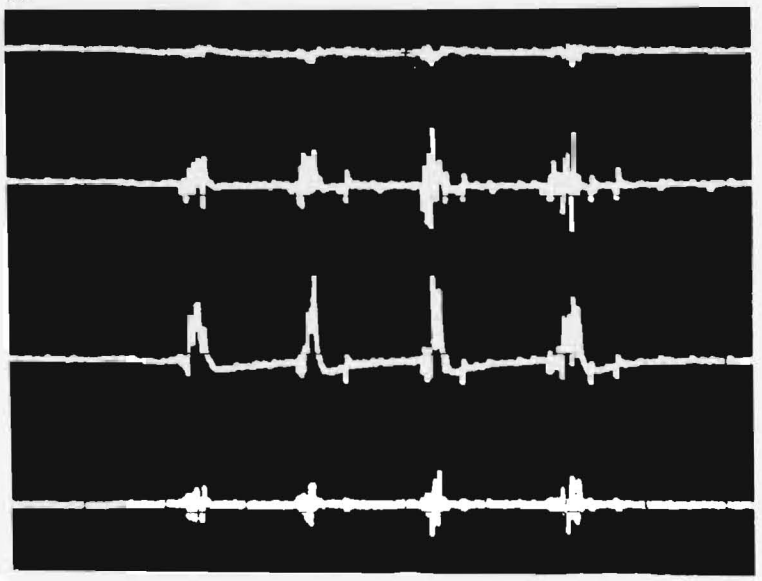
Myogram activity evoked reflexively in muscle M-21 in response to imposed movements of the whole mandible.

(a) Imposed rapid opening of the left mandible. Trace [i] right M-21; [ii-iv] three different sites in the left M-21. Calibration 0.5s.

(b) Left mandible pulled open by a loop over the cusp region. Recordings from the left (l) and right (r) M-21. Calibration 1 second.

(c) Upper traces - three brief pulls on the left mandible, recording conditions as in (b). Lower traces - three brief pulls on the right mandible, recording conditions as in (b).

a

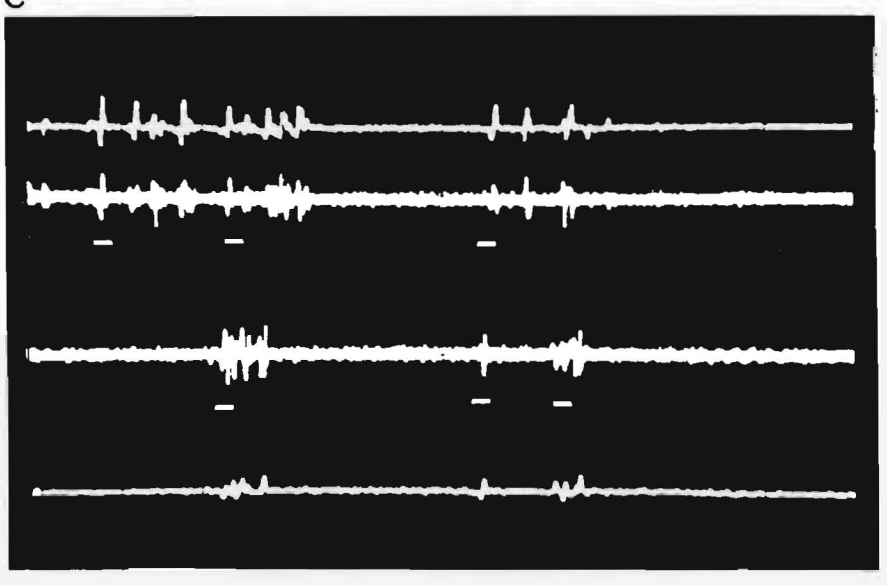


0.5s

b

1.0s

c



0.2s

CHAPTER V

NATURE OF FEEDBACK REQUIRED GIVEN THE OBSERVED BEHAVIOUR OF THE JOINT

Before examining the sense organs of the mandibular joint I wish to consider the possible requirements of the system. The mandible is an exceedingly simple appendage - a simple lever with only one moving section unlike the 5-part walking leg of the insect. The mandible has its movements confined largely to a single plane by the uniaxial dicondylic joint. In its simplicity the single mandible most closely resembles the dactylus of the crab cheliped, with which it shares some common functions in both feeding and defence. Unlike the crab dactylus the mandible is not rigidly confined to a single plane of movement. The movement is normally restricted to a single plane by the presence of two articulations. The contact is maintained in these largely by the forces of the various mandibular muscles, rather than being confined by rigid skeletal structure. The articulations can therefore be dislocated if sufficient force is applied. From the thegosis marks found particularly on the adult males it is apparent that during forceful closure one or both mandibles can dislocate in the extreme closed position. In short, the mandible normally moves in a fixed plane but may at one extreme of its excursion be displaced from this plane. Almost any displacement of this sort is likely to alter the length of a receptor spanning

the joint. This is certainly true of the VMRO which is aligned obliquely across the joint.

One requirement of the receptor system may be to discriminate directions of movement to counteract this potential ambiguity. This would require central processing of an additional input, either a stretch receptor or a receptor monitor contact at the articulation.

While biting may still seem to involve simple movements of simple appendages the paired apposable arrangement of the mandibles greatly increases the complexity of their operation. Several variables are introduced. Firstly the position in which one mandible will contact the other is not fixed. It is not sufficient to monitor the angle between the mandible and the head capsule to determine when and where contact will be made with the apposing mandible, as it, too, is independently moveable. It follows from this that the contour of the meeting surfaces may vary, a restricting condition for the weta where the mandibles cannot close fully unless the complementary cusp pattern of the two mandibles are matched. The feeding bite, which involves shearing rather than crushing would be ineffective unless the mandibles met appropriately.

A further requirement for effective biting is that an approximately equal force be developed on each mandible. This is particularly true of the most powerful bites. Any departure from this situation must result in displacement of the weaker mandible. A static positional equilibrium could perhaps be maintained by position-monitoring sense organs. However any such

system has to be able to maintain the constant position, and consequently equalise the forces over a wide range of force. The adult male weta can develop in excess of 1000gm.cm torque in each mandible, measured during biting against an isometric lever. From the weakest chewing movements of the softest food up to this limit is a range of approximately 0-1000 and effective biting with the mandibles in more or less constant positions can be achieved throughout it.

The development of force does not occur absolutely isometrically, nor is it perfectly synchronised between the two mandibles. The patterns of movement during feeding (see Chapter III) are essentially shearing movements in which the left mandible may often be displaced (enforced movement in the "opening" sense). This indicates an imbalance of forces (or a mechanical disadvantage in the meeting of the mandibles) presumably necessary and perhaps carefully controlled. Only at the very completion of a full closure bite does the truly isometric condition apply. Can the observed behaviour be achieved through a positional control system or must a tension monitoring component be included as well?

Immediately the concept of more than one component is introduced, several questions arise. Are all the components monitored at all parts of chew/bite cycle? Does their relative importance remain the same throughout the cycle? What is the function of the sensory input - continuous monitoring, positive or negative feedback, switching, or safety limit setting? Are the parameters

under consideration appropriate to the functioning of the system? The Ia afferent of the vertebrate muscle spindle has long been regarded as an element in a load-compensating length monitor. Recently Houk (1979) has suggested that regulation of a property he termed "stiffness", the ratio of force change to length change is more appropriate to the understanding of vertebrate skeletal muscle control. The mandibular mechanism has so far been discussed in terms of position and tension but these may not be adequate descriptors of the feedback system.

Earlier the need for appropriate meeting of the two mandibles was emphasised in terms of control of relative position. While this may be important, the precision of occlusion may well depend on feedback from receptors in the areas of contact. The nature of the feedback, whether positive or negative, might then depend less on the individual unit than on the broad field pattern of discharge. That is, a given receptor might have either an excitatory or an inhibitory central influence depending on what other units were stimulated in synchrony with it. Although the cusp region of the mandibles of other insects receives a sensory innervation it cannot be assumed that this is their function. Mandibular contact may be a necessary condition for the onset of full tension development (total muscle activity), or at least for rapid tension development, thereby having a gating function. Rather than acting as a switch the cusp receptors may simply produce feedback augmenting tension development as is found in the cuticle

strain receptors of the locust tibia (Heitler and Burrows, 1977). The behavioural studies (Chapter III) have shown that during closure to contact mismatches can be made to the extent that the right mandible overlaps the left. When this occurs it appears that full tension is not developed and the mismatching may be corrected without a complete opening being necessary. This suggests that cusp receptors may be involved in the control of force development, perhaps having the power to inhibit it.

The coordinating role of the sense organs has so far been viewed as fine tuning of an intrinsic motor programme to achieve more precise control of the structure containing the sense organ. This assumes that all the mouthpart behaviour is controlled by a central motor programme. A second means of controlling behaviour is via sensory-mediated reflexes. The two mechanisms are not mutually exclusive. Feeding behaviour, in particular, requires the coordination of several mouthparts in a constant phase relationship at varying frequencies. Distributed reflexes as found in rock lobster (Clarac et al, 1978) may contribute to this. Less extensive than the broad, intersegmental influence is the crossed reflex, here implying the modification of mandibular muscle activity by afference from the contralateral mandible. The morphological and behavioural asymmetry of the two mandibles suggests that one might reflexively influence the phasing or amplitude of the other. The interdependence of mandibular functioning already alluded to is perhaps

achieved by reflexive control, rather than by central comparison of the two outputs.

What further requirements are introduced when the nature of the object being bitten is considered? Size, shape, surface texture and consistency are all mechanical parameters which might be important. It is quite possible that most of the information on the first three of these comes mainly from the other mouthparts, particularly the maxillae with their major role in the manipulation of food particles. The consistency of the object, particularly of food, may present a more complex problem. Similar patterns of regular consistent mastication have been observed with foods as different as overripe apple and cooked chicken. The similarity in pattern combined with the textural difference clearly suggests that some form of load-compensation system is operating. An equivalent of the vertebrate spindle where efferent input continuously altered the set-point of the receptor could produce such a pattern. The sensor need not necessarily monitor displacement. A muscle-receptor with tension-sensitive elements could also register tension variations if a programmed shortening (i.e. mandible closure) were restrained. The variable loads presented by foods of different consistency therefore seem to require an error-detecting feed-back system, which can potentially be subserved by length or tension-sensitive elements.

The unpredictability of food consistency creates a safety problem. What happens when a resistant rigid structure suddenly collapses? Do the unloaded mandibles

rapidly snap together, or is there a limiting mechanism? This may not be a great problem for the weta although the presence in the gut of beetle larvae with their particularly sclerotised head capsules suggests that some food may have these properties.

The possibility of damage from sudden changes in resistance is not the only hazard presented by the object. There are many substances which are harder than even the heavily sclerotised cuticle of the cusp region. Local cuticular sensilla are probably best suited to detecting grit taken up with or within food and hard objects encountered in defensive biting.

The highly-developed and powerful mandibular musculature represents a further potential cause of damage. The stress of full-force biting visibly distorts the head capsule and abrasion of the cusp region is apparent on many animals. Sensory feedback may play a role in the prevention of self-inflicted injury. Huge forces are applied to the mandible mainly by a single large adductor muscle which inserts onto an apodeme constructed of heavily tanned cuticle. This rigid structure connects to the mandible by a flexible coupling of softer cuticle (Chapter IV). As both the coupling and the apodeme are subject to the full extremes of muscle tension they might be expected to possess safety-monitoring sensory input.

These same forces are transmitted to the region of mandibular occlusion, the cusp region. Here the mandible approximates to a tapering curved tube. The applied forces would tend to collapse the tube by

lateral pressure and to bend it by shearing forces approximately at right angles to the long axis of the mandible. Occasional snapping of the tip in experiments where the mandible had been weakened by local injury suggests that the mechanical safety factor is not high. There is no absolute necessity for this sort of hazard to be monitored by the sensory system as it may be counteracted by strengthening the cuticle but this possibility needs to be kept in mind when considering the possible feedbacks.

Earlier it was mentioned that the articulations are capable of being dislocated. This may well be under sensory monitoring. In any case the articulations, being the fulcrum in the lever system might well have stress or strain detectors associated with them, either on the head capsule or on the mandible.

All the preceding issues have been considered in terms of mandibular closure, yet the control ofopening, or abduction is also crucial. Efficient mastication requires that the mandibles be opened no wider than necessary, both to facilitate food retention and minimize energy wastage. Even if the assessment of food size is a role of the other mouthparts the mandible opening must be monitored internally. Possibly loss of cusp contact may aid in initiating a closure cycle. Despite this there is a complete behaviour that involves controlled mandibular opening - the mouthpart gaping in the threat display. Here the extremes of abduction are reached with each mandible being moved up to 45^{o} from the midline. These positions may be maintained for several minutes.

With no external loads involved and a posture that is often static this may be purely a question of positional control.

We have here considered only three of the variety of known mandibular behaviours. Through examining just three it is possible to see some of the requirements of these apparently simple appendages. While they are essentially simple levers moving through a restricted angle in a single plane and having no role in the maintenance of posture, several special requirements may be made of them. An isotonic contraction under minimal load may rapidly become isometric with the development of high levels of tension. Effective biting may require precisely-phased alterations in force and position or in some parameter related to these. Diverse mechanical properties of the object bitten may lead to their recruitment of additional muscle activity or to inhibition, particularly if injury is to be avoided. The forces the muscles can produce may well have created the potential for self-injury.

These are only some of the possible roles of the mandibular proprioceptors. Other behaviours may well have different requirements, as in the weak mandibular movements involved in drinking. All these possibilities deserve inclusion when considering the possible functioning of the various receptor elements involved in peripheral feedback. The strong bias toward mechanical function assumed in this discussion raises one further question. Does the peculiar array of receptors found in the mandible represent a unique response to a unique set of

criteria, or does it simply reflect the evolutionary inheritance of primitive mandibulate insects?

CHAPTER VI

THE SENSE ORGANS OF THE MANDIBLE

I THE ANATOMY AND PHYSIOLOGY OF THE VENTRAL MUSCLE RECEPTOR ORGAN

(1) Anatomy

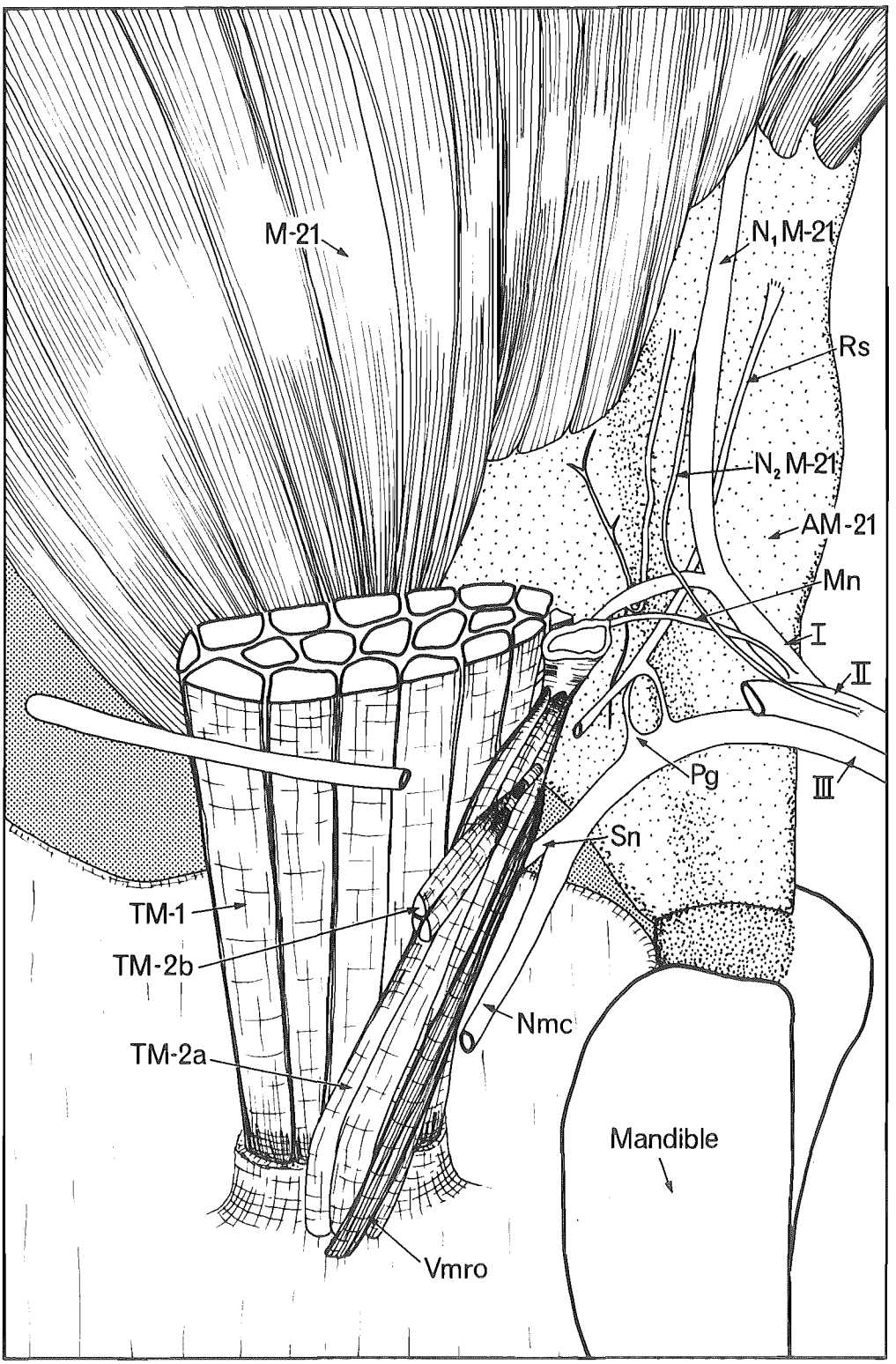
The ventral muscle receptor organ (VMRO) is a complex stretch receptor spanning the joint between the mandible and the head capsule (Figure 24). Part of the tentoro-mandibular complex, the VMRO lies along the medial margin of muscle TM-2a. It is a thin muscle differing in internal structure from the adjacent skeletal muscle. Distributed along its length are more than 80 sensory neurones with dendrites penetrating into the muscle fibres.

The VMRO is contiguous with muscle TM-2a throughout its length, although the origins and insertions of the two are quite distinct. The origin of the VMRO is a small apodeme attached to the anterior arm of the tentorium immediately posterior to the TM-2a. From here the VMRO curves approximately 180^{o} around the parallel muscle to insert into a small pit in the cuticle immediately anterior to the parallel muscle insertion (Figure 24). Despite their proximity the sense organ and muscle are not physically attached although the muscular core of the VMRO suggests that it may be derived from the adjacent muscle. Where the VMRO passes over the cuticular ridge receiving the insertion of

Figure 24

The tentoro-mandibular musculature and associated nerves as revealed by frontal dissection.

AM-21 - apodeme of muscle M-21; Mn - motor nerve to TM-1, TM-2a and the VMRO; N_1M-21 - major motor nerve to muscle M-21; N_2M-21 - small nerve from trunk II also supplying muscle M-21; Nmc - nerve to the cusps and more distal parts of the mandible; Pg - group of cell bodies supplying the apodeme strand receptor; Rs - receptor strand of the apodeme strand receptor; Sn - sensory nerve from the VMRO; VMRO - ventral muscle receptor organ; I, II, III - major mandibular nerve trunks running from the suboesophageal ganglion.


M-21
N₁M-21
Rs
N₂M-21
AM-21
Mn
I
II
III
Pg
Sn
TM-1
TM-2b
TM-2a
Nmc
Mandible
Vmro

of muscle TM-1 it bends slightly. Both this deflection and the curvature round muscle TM-2a mean that the VMRO is not a straight strand of tissue.

The VMRO spans the mandibular joint at an oblique and varying angle. With the mandibles in the rest position the receptor axis lies at an angle of approximately 50^{o} to the plane of opening. As the mandible is abducted through an angle of 40^{o} the angle between the receptor axis and the plane of opening decreases to approximately 33^{o}. At the same time the receptor length increases from 2.4mm to 3.35mm in a mature male weta, a length change of approximately 40 percent.

In transverse section the VMRO is typically almost circular reaching a diameter of approximately 70 microns in the region where there is the greatest aggregation of sensory axons. There is little longitudinal differentiation in diameter or internal structure.

Most of the essential elements of internal structure are represented in Figure 25, a transverse section made just distal to the region where the sensory nerve joins the receptor. Five major components of the sense organ can readily be distinguished. Two sensory cell bodies are the most prominent structures. Occupying approximately one third of the cross sectional area is a large tract of sensory axons of widely-varying diameter. Most of the rest of the inner region of the receptor is occupied by the highly-dissected muscle fibres and interspersed profiles of sensory and

Figure 25

Transverse section of the ventral muscle receptor organ.

The section has been made just distal to the junction with the sensory nerve and proximal to the point of entry of the motor nerve.

The five regions referred to in the text are:

(1) the muscle fibre tract (mft)

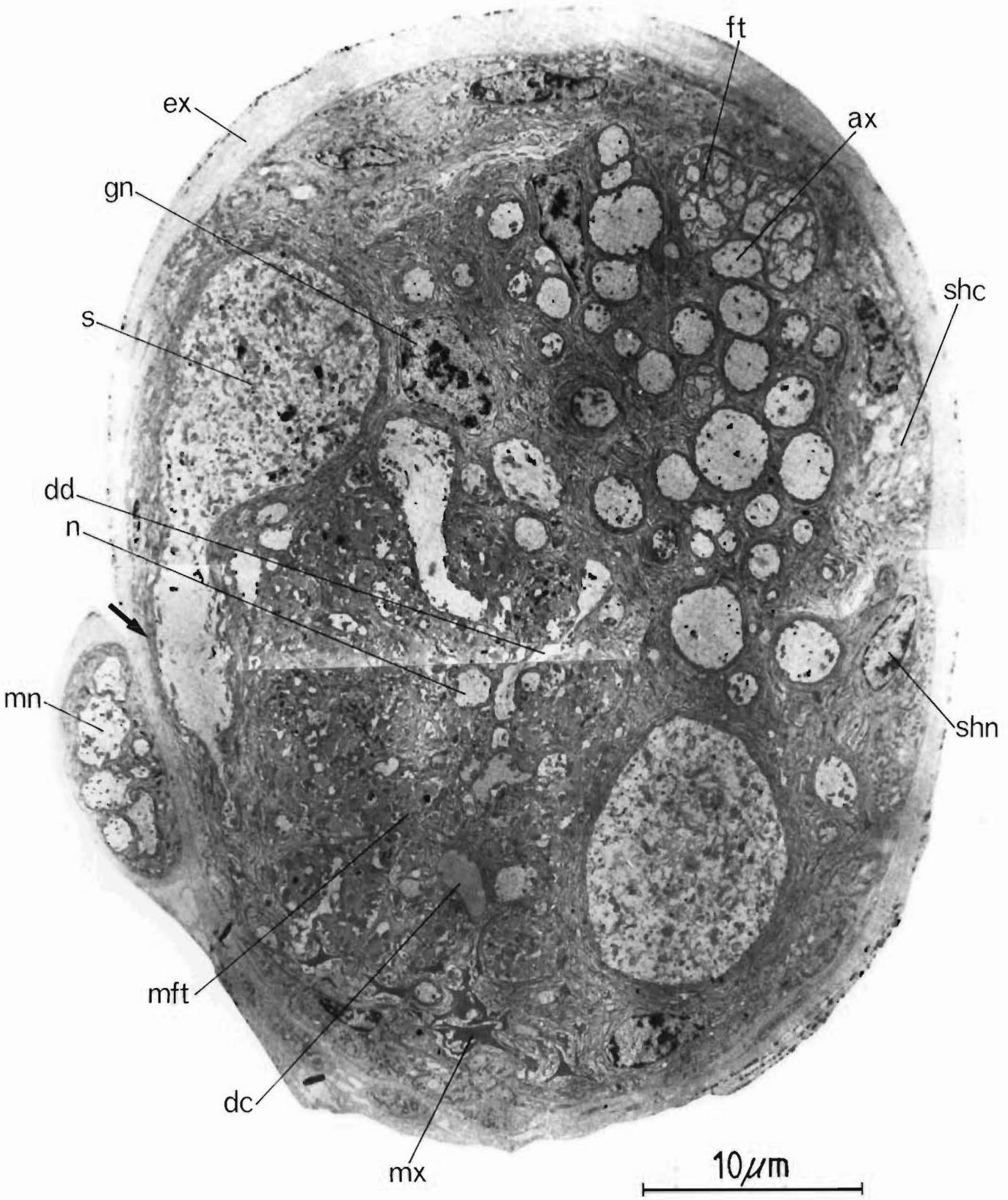
(2) the sensory cell bodies (s)

(3) the sensory axonal tract, opposite the muscle fibre tract

(4) the surrounding layer, comprising the sheath cells (shc) and the extracellular layer (exl)

(5) the motor nerve (mn)

Abbreviations: ax - sensory axon; dc - cell in muscle fibre tract with densely-staining contents; dd - dendritic profile; exl - extracellular fibrous surrounding layer; ft - tract of small nerve fibres which may include dendritic endings; gn - glial cell nucleus; mft - msucle fibre tract; mn - motor nerve; mx - dense extracellular matrix; n - neural profile in muscle fibre tract; s - sensory cell bodies; shc - sheath cells; shn - sheath cell nucleus. The arrow indicates a minimal sheath cell layer thickness.


ft
ex
ax
gn
shc
s
dd
n
mn
shn
mft
dc
mx
10μm

motor axons. Surrounding all these structures is a distinctive layer of sheath cells which is bounded in turn by an extracellular matrix of collagen-like material. The fifth component is the nerve containing the motor axons. In Figure 25 it has been sectioned just proximal to where it joins the sense organ. The constituents at these five regions will now be considered in more detail and any longitudinal variation in the observed pattern noted.

(a) The muscle fibre tract. The muscle fibre tract is an anastomosing network, and the number of constituent elements is not discernible from any one section. Careful examination of Figure 25 reveals a number of muscle fibre profiles. The shapes and sizes of these vary greatly, this irregularity being the only unifying characteristic of their shape. The largest appear amoeboid in section with narrow processes linking larger regions which in turn interdigitate with other muscle fibres, neural elements and glial cells. The smallest profiles may be only 1-2μm and recognisable only by a few scattered myofilaments. A section further down the receptor had a similar appearance but few of the more distinctive elements of the original pattern remained. The larger profiles had broken into several smaller units, others had coalesced and the smallest profiles appeared in localities far removed from in the first section. Sections from the more proximal region of the receptor revealed a lesser number of elements with profiles tending towards circularity. These converged on an apodeme-like process in some preparations,

Figure 26

Ultrastructure of the ventral muscle receptor organ.

(a) A terminal bouton of a motor neurone situated on the surface of a muscle fibre. The arrows indicate proximity to synaptic sites. The boutons contain transmitter vesicles, dense cored vesicles and mitochondria (mi). Glial cells (gl) cover the nerve ending where it is not in contact with the muscle fibre. sr - sarcoplasmic reticulum.

Calibration 1μm

(b) Transverse section of the receptor muscle fibre showing the irregular array of thick filaments in which hexagonal groupings (circled) can be distinguished. Thin filament groupings of 12-13 can also be found.

Calibration 0.2μm

(c) Transverse section of part of a muscle fibre showing a nucleus. The small muscle profiles are probably all part of the same fibre. Several diads are visible (arrows).

Calibration 1μm

(d) Longitudinal section of a receptor muscle fibre being penetrated by a dendrite (dd) in which both microtubules and mitochondria are visible. A fine dendrite ending (de) approaches the darkly-staining Z-disc material (z). Glycogen-like granules (g) are present in the Z-disc region.

Calibration 0.5μm

(e) Motor end plate region opposite the Z-disc material (z) of a receptor muscle fibre cut in longitudinal section. sr - sarcoplasmic reticulum; g - glycogen-like granules.

Calibration 0.2μm

(f) Section through a probable synaptic site on the receptor muscle fibre. Endoplasmic reticulum (er), multivesicular bodies (mv), mitochondria (mi) and dense-cored vesicles (dc) are present in addition to the electron-lucent transmitter vesicles.

Calibration 0.2μm

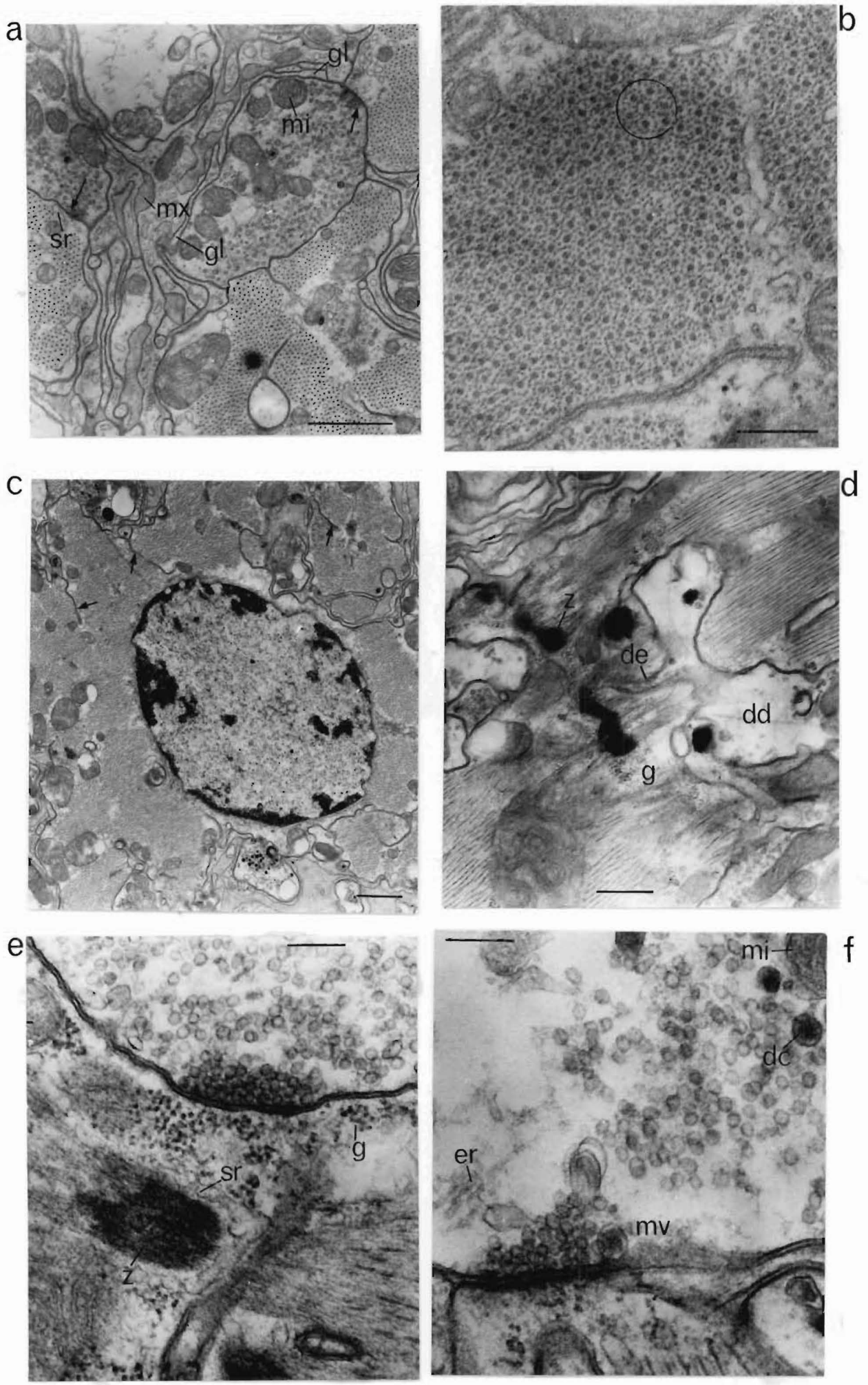


Figure 27

Ultrastructure of the ventral muscle receptor organ.

(a) A primary sensory cell, characterised by a large nucleus and peripheral location in the receptor. It is surrounded by alternating layers of glial cells and granular extracellular matrix.

Calibration 0.5µm

(b) The motor nerve lying just outside the VMRO. There are three large and three small axonal profiles.

Calibration 3µm

(c) Detail of the axonal tract showing the extensive glial cell development and the granular extracellular matrix.

Calibration 1.5µm

(d) Detail of the axonal tract showing proliferation of the extracellular matrix (mx).

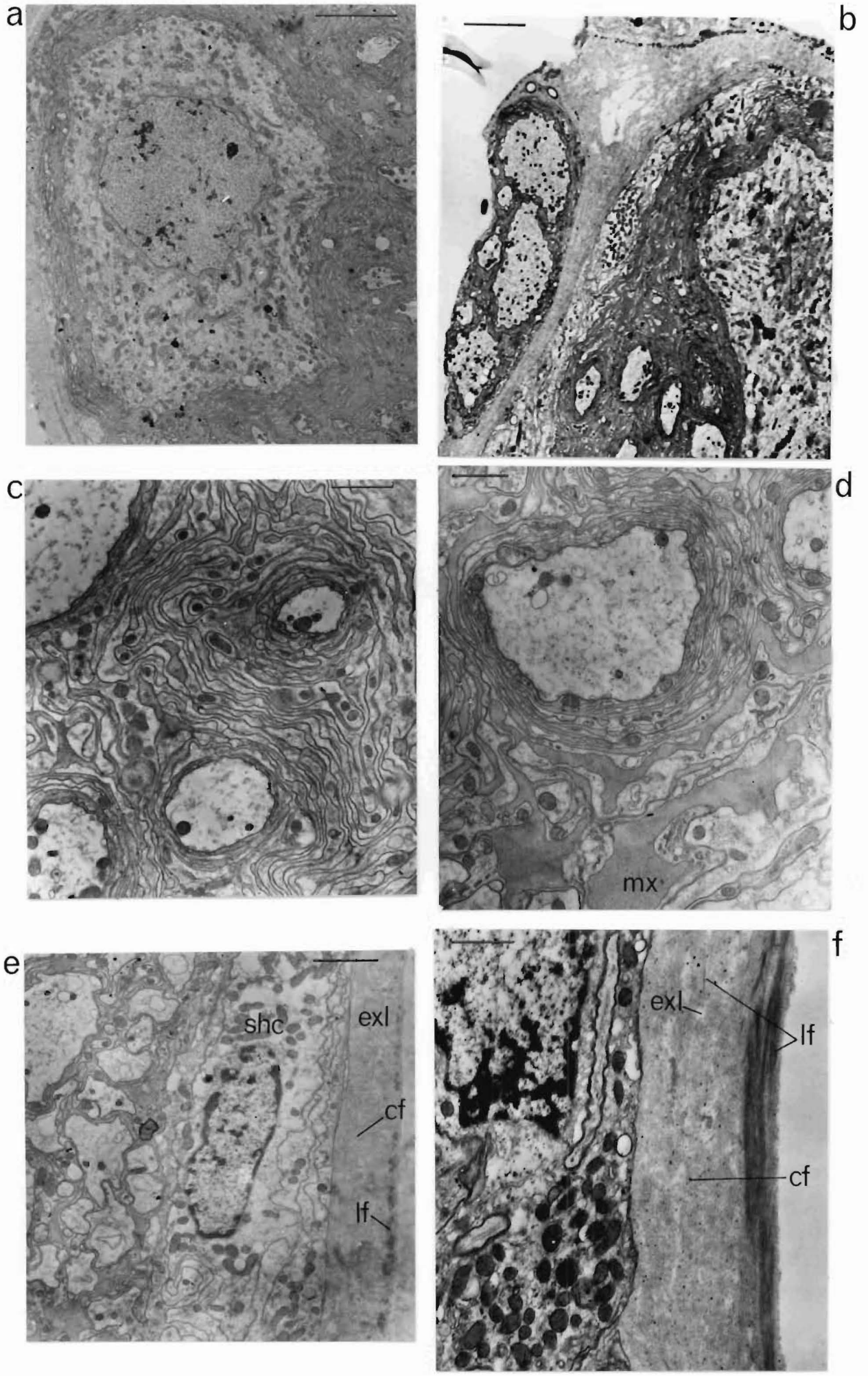
Calibration 1µm

(e) Transverse section through the surrounding layer showing sheath cells (shc) with an elongate nucleus. The layer of sheath cells is several cells thick in places. External to this is the extracellular layer (exl) with scattered circumferentially-oriented fibres (cf) and denser tracts of longitudinal fibres (lf) in the periphery.

Calibration 2µm

(f) Longitudinal section through the surrounding layer where it is one cell thick. Dense aggregations of mitochondria are visible. Longitudinal fibres (lf) are scattered throughout the extracellular layer (exl) as well as being concentrated in the periphery. Circumferential fibres are seen in section scattered throughout the layer.

Calibration 1µm


a
b
c
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mx
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shc
exl
cf
lf
f
exl
lf
cf

while in others they appeared, under the dissecting microscope, to have arisen directly from the tentorium. While the muscle fibres appear as distinct elements in any one section it is not known whether they sustain an individual identity or become linked into a single syncytium along the length of the receptor. The loosely-intermeshing structure is sustained along most of the length of the receptor. In the most distal region the proportion of cross-sectional area occupied by muscle fibres is much reduced, while neural profiles remain prominent, but not numerous.

Detailed examination of the internal structure of the muscle fibre reveals a distinctive structure, different in many ways from the adjacent skeletal muscle. The distribution of myofilaments across the profile was often discontinuous, with large areas lacking filaments altogether. These regions often did not appear to be occupied by any distinct cellular organelle, as in the spaces close to the sarcolemma (Figure 26a). Myofibrils were irregular in size and shape although many were approximately circular or polygonal in transverse section with diameters of about 0.3-0.8μm. They were separated from one another by mitochondria, sparsely developed sarcoplasmic reticulum, by sarcoplasm and occasional T-tubules (Figure 26a,b,c). Diads were most commonly found (Figure 26c).

Hexagonal groupings of thick filaments could often be discerned within the more irregular array (Figure 26b). A regular pattern was never sustained over all of any cross section. The thin filaments were arranged around

the thick filaments in irregular circ les of 12-13.

The location of nuclei was hard to define in such an irregular fibre structure, but they appeared to be centrally positioned (Figure 26c).

The general appearance of the receptor organ muscle fibres is in marked contrast to that of the skeletal muscle fibres of the tentoro-mandibular complex. Fibres from muscle TM-2b are shown in Figure 34e. Gone is the extensively dissected profile. The fibres are compact and polygonal with radially arranged fibrils delineated by transverse tubules. Virtually the whole cross section is occupied by filaments, mitochondria or the peripheral nucleus.

Further aspects of the disordered structure are revealed when the receptor muscle fibres are viewed in longitudinal section. The Z-discs appear as small islands of densely-staining material with large gaps between them. Often these were filled with cytoplasm containing dark glycogen-like granules (Figure 26d). The patches of Z-disc were commonly roughly aligned to form a disc region spanning the fibre but this line was often not parallel with the equivalent line delineating the other end of the sarcomere. This made sarcomere length measurements somewhat arbitrary, but values around 7μm were obtained from material fixed in situ in alcoholic Bouin's.

The diffuse nature of the Z-disc and the lack of registration with adjacent fibres means that sarcomeres may be difficult to distinguish with the light microscope, whereas they are clearly discernible in skeletal muscle.

Synapses were commonly found in close proximity to the Z-discs (Figure 26e). While the terminal boutons were large and might span a complete sarcomere, the synaptic regions proper were much smaller, perhaps 0.5µm across. They were characterised by very dense aggregations of vesicles aligned on the presynaptic membrane (Figure 26e,f). The vesicles were almost circular to oval in section and approximately 250-500Å in diameter.

While various other vesicle types, such as larger dense-cored vesicles and multi-vesicular structures were present in the same bouton (Figure 26f) only one obvious type of electron-lucent transmitter vesicle was found. Mitochondria and, less commonly, endoplasmic reticulum were also found in boutons, which were usually enclosed in thin processes of one to several glial cells (Figure 26a). Beyond this layer were other glial cells or a dense granular extracellular matrix (Figure 26a).

Boutons were commonly found on the surface of muscle fibres but occasionally were largely enclosed by fibres. Here it appeared to be several portions of the fibre network surrounding a bouton, rather than an invagination of a single fibre. Infrequently, synapses were found on processes of the muscle fibres which did not contain filaments in close proximity.

Densely staining granules resembling glycogen granules were found close to the post synaptic membrane. Mitochondria are usually adjacent. Sarcoplasmic reticulum was usually present without being extensively developed (Figure 26a,e).

Throughout the muscle fibre tract were glial-type cells, cells with densely-staining granular contents (Figure 25), an extracellular matrix of very similar appearance and numerous neural profiles.

(b) The primary receptor cells. These multipolar sensory cells are distributed more or less regularly throughout most of the length of the receptor. They are less frequently encountered in the proximal 15% of the receptor. Cobalt backfilling of the sensory nerve revealed more than 50 in one preparation. Counting axonal profiles in the sensory nerve as it joins the VMRO revealed 90-110 larger profiles in several adult wetas. Adding the smaller profiles, which may be less than one micron in diameter, raised the number to between 150 and 170.

The cell bodies themselves are situated peripherally in a cross-section of the receptor. They are readily distinguished by the large cytoplasmic mass with a large central nucleus (Figures 25, 27a). The soma is invested with several consecutive layers of ensheathing glial cells, including those with dense granular cytoplasm (Figure 27a). While some of this substance is definitely membrane bound, there appears to be an extensive extracellular matrix with a closely comparable appearance. The axonal profiles are enveloped in a similar manner.

The sensory dendrites branch and permeate the adjacent muscle fibre tract (Figures 25, 26d). Large naked dendrite profiles intimately enclosed in muscle fibres are encountered in longitudinal sections (Figure 26d). These may ramify extensively throughout

the fibres, even passing through Z-disc regions. However, a proportion of dendritic endings terminate in the region of the Z-disc. Figure 26d is part of a series of serial sections showing such an ending. Such small profiles are frequently encountered, particularly near the Z-discs. As these typically have no neurotubules they cannot be identified unequivocally as dendritic endings without serial sectioning. The confirmed dendritic endings have no detectable internal contents. Ciliary structures are not found. Once a dendrite begins to penetrate a muscle cell the glial sheath is lost and the terminal regions are naked. No accessory structure, apart from the muscle cell, is associated with the dendritic endings, either intra- or extra-cellularly. The possibility of additional locations for dendritic endings must be considered. Fine processes have been observed within the tract of nerve fibres. Many of these are clustered in closely-aggregated tracts and may simply be very small axonal profiles (Figure 25). However, occasionally small profiles, devoid of structured contents, have been observed embedded in the granular matrix associated with the glial cells of the axonal tract (see below). The possibility that there are some dendritic endings embedded in non-contractile tissue cannot be excluded.

In addition to the cell bodies found within the receptor, vital staining with methylene blue has revealed a large, multipolar neurone lying between the receptor and the sensory nerve where these meet. The cell body was not contained within either the nerve

or the receptor organ but sent processes into each. Three separate processes, presumably dendrites, appeared to enter the proximal portion of the VMRO. A fourth process entered the sensory nerve shortly after it left the VMRO. No further details are known.

(c) The neural tract. An aggregation of neural profiles occupies approximately one quarter of the cross-sectional area of the muscle receptor (Figure 25). At the level of the section illustrated, this is the medial portion of the receptor and it leaves the receptor about one third of the way from the insertion to form the sensory nerve (Figure 25). This joins the nerve supplying the more distal parts of the mandibular cuticle to form nerve trunk III. Rarely, the sensory nerve has been found to leave the receptor at two different levels along its medial margin. These two branches fuse before joining nerve trunk III.

Within the receptor the number of profiles varies with the level at which the section is made. It is greatest where the sensory nerve leaves the receptor, where more than 170 profiles have been counted, but even in the more distal regions where there is little evidence of muscle fibre development more than 20 profiles have been counted. While the tract must consist largely of sensory axons, the possible presence of sensory dendrites, as discussed above, and also motor axons cannot be excluded.

All fibres within the tract are invested in multiple layers of glial cells (Figure 27c). Several large glial cell nuclei are visible in Figure 25 . Between the enveloping cells the spaces are filled with a densely-

staining matrix which may be expanded to a greater thickness than the glial cells (Figure 27d). Similar matrices are associated with neural elements on the periphery of the muscle fibre tract in Figure 25.

(d) Surrounding layers. In addition to the specialised cells surrounding the neurons the entire sense organ is enclosed in a layer of sheath cells of a distinct type. These presumably produce the outer connective tissue layer which completely encloses all the cellular components of the sense organ (Figure 25). The sheath cells (Figures 27e,f) typically have large elongate nuclei similar to the glial cell nuclei and large numbers of mitochondria. The sheath layer may be only one cell layer thick (Figure 27f) or several layers overlapping where the cells meet (Figure 27e). The thickness of the layer varies considerably. A minimal covering is shown in the region between the motor nerve and the sensory dendrite (arrowed) in Figure 25. There is no densely-staining extracellular matrix between the sheath cells, adjacent membranes being closely applied.

The outer connective tissue layer is completely non-cellular and appears equivalent to the neural lamella. It contains fibrous elements exhibiting a collagen-like periodicity. The longitudinal and transverse sections in Figures 27e and f illustrate the orientation of these fibres. Clusters of longitudinally-oriented fibres are found close to the periphery of the layer, as well as smaller, more-scattered groups with similar orientation being found throughout the layer. Small groups of circumferentially-oriented fibres are

found distributed regularly throughout the layer. Intermediate orientations are encountered and much of the matrix appears granular but non-fibrous.

(e) The motor nerve. The motor nerve to the VMRO is a branch of the nerve supplying muscles TM-1 and TM-2a, the axons leaving the suboesophageal ganglion in trunk I (Figure 24). In the experimental preparations the motor nerve to these components of the tentoro-mandibular complex is obscured by the tentorium. The fine branch to the VMRO enters the sense organ on the opposite side to the sensory nerve. It is hidden from view behind TM-1 and TM-2a in Figure 24. The efferent supply to the receptor is accessible to the experimenter only in the basal regions of nerve trunk I.

The motor neurons appear in Figure 25 in a small nerve on the periphery of the sense organ. Seven axonal profiles are present; 3 large, 2 intermediate and 2 smaller. The pattern of 3 large profiles is repeated in Figure 27b, taken from a different animal, but here only 3 small profiles are present. The 3 large axons have been traced into the sense organ and found to branch without a cell body being encountered. The destination of the small axons is unknown, as is their identity. They may be sensory or motor. The reason for the variation in number is not known.

Confirmation of the route of the motor input came from simple physiological experiments. Cutting nerve trunk I removed all the larger unit responses and many of the small units recorded from the sensory nerve (Figure 30). All the phasic activity in a constant

position was lost. Transecting nerve trunk III appeared to have no influence on the phasic responses. Patterns of activity recorded before transection using hook electrodes were essentially the same as those recorded from the distal portion of the cut sensory nerve using a suction electrode, although individual units could not be identified in both preparations. Anatomical and physiological techniques failed to reveal any motor neuron to the VMRO in nerve trunk III.

It thus appears that the VMRO has at least three and up to six or seven motor neurons which enter the sense organ from a branch of the nerve supplying muscles TM-1 and TM-2a. The additional three or four axons may be sensory. Details of the innervation pattern of the muscle fibres are not known.

(2) Physiology of the ventral muscle receptor organ

The results presented here summarise the findings from 10 preparations.

The activity of the VMRO is critically dependent on the state of reduction of the preparation. Responses are altered markedly upon section of both the circum-oesophageal connectives and the motor nerves. Following section of the motor nerve to the VMRO, only some of the smallest units continued to respond. Cutting a circum-oesophageal connective decreased the general activity of the preparation. The gut was much less active and powerful bites were less likely to be produced. The VMRO output was less likely to show spontaneous changes unrelated to applied stimuli. In general an intact

preparation, with no major nerves cut, was used where possible. Any departure from this is noted in the text. Imposed mandibular opening invariably had an excitatory effect on many VMRO units. The responses from a preparation where all major nerves were left intact is shown in Figure 28. The basal level of discharge with both mandibles in the 'rest' position consisted of a number of small tonic units and a continuous discharge of slightly larger units firing in a more or less regular but bursty rhythm. The frequency of bursts was about 4 per second. The bursts appeared to comprise more than one unit, in some cases (Figure 28a). Holding the mandible open 18^{o} altered the level of ongoing activity in two ways. The bursts of spikes continued at about the same rate but larger amplitude units were recruited (Figure 28b). It is now evident that the bursting pattern is not highly consistent, a maintained position leading to spontaneous increases and decreases in firing rate. In addition there were sporadic bursts of high frequency discharge recruiting still larger units (Figures 28b,c,e; 29a,b). These bursts became more frequent at wider angles of opening, yet were not necessarily linked in any particular phase to an imposed movement. Progressive imposed opening of the mandible elicited higher levels of tonic discharge, the short bursts becoming longer and more frequent until at the widest angles the burst pattern developed into continuous discharge (Figure 28c). This was still capable of central modulation as can be seen in the final two sequences.

Sectioning the circumoesophageal connectives reduces the level of output from the VMRO. It also reduces the level of activity of the gut and the mandibular musculature in general, including the tentoro-mandibular muscle. Following section of the right connective both tonic activity and the larger bursts still occurred (Figure 29a). This record, from a different preparation is from a tonic unit which was excited by opening and inhibited during passive closure with brief bursts of phasic activity. The mandible was here held in a fixed position. Note that the tonic unit was inhibited after the phasic burst. Simultaneous recordings from the same VMRO nerve and from a tungsten pin myogram electrode inserted in the VMRO itself showed synchronous phasic bursts of potentials, the sensory response developing shortly after the myograms. The two ceased almost in unison. While the myogram electrode was definitely located in the VMRO it is not certain that the recorded potentials were purely from the VMRO. Synchronous bursts were recorded from other parts of the tentoro-mandibular musculature. Similar coincidence between TM-myograms and VMRO sensory discharge was routinely recorded. Sectioning nerve I, which contains the TM and VMRO motor neurons abolished the phasic bursting of the sensory discharge in maintained position and reduced the number of tonically active units.

The sporadic 0.5-2.0 second bursts of larger units typically encountered with the mandible partially opened appeared to depend on the level of central excitation.

Figure 30a showed the VMRO response to passive

right mandible opening in a preparation where both circumoesophageal connectives were cut, as was nerve II. This eliminated input from the DMRO and the various receptors associated with the anterior articulation and probably also any from the posterior articulation. Opening elicited an excitatory response. The largest units still showed phasic components which were not apparently linked to periods of change in mandible position. They were superimposed on a tonic excitation in response to different maintained angles of opening. Note that while there were phasic bursts at the 13^{o} angle, there was no response of the largest unit to movement from 13^{o} to 26^{o}, although some of the smaller units increased their discharge as soon as movement was begun.

The almost total reduction in activity which resulted from cutting nerve I is shown in Figure 30b. Here the largest units have been emphasised as in the preceding trace.

There was a low level tonic response with a weakly phasic response during the opening movements. None of the larger units responded. There was a low level tonic discharge with a weakly-phasic response during the opening movements. All these units were too small to have been visible in the general discharge of many slightly larger units which responded to enforced opening when the motor neuron supply was still intact.

The VMRO input is influenced reflexively by input from other sensory sources. The inhibitory effect of enforced opening of the left mandible is shown in Figure 28d. The recording was from the right VMRO

with the mandible held open 23° from the rest position. As the left mandible was progressively opened the larger units which were earlier shown to be excited by ipsilateral opening were inhibited by contralateral opening. Inhibition was complete when the left mandible had opened to approximately the same extent as the right. This inhibition does not apply to all units. A small tonic unit was firing at 8-10Hz in the last three left mandible positions without obvious modulation, although it appeared to be inhibited during left mandible closing (Figure 28e). Inhibition of this unit accompanying left mandible closure was also found during cyclical oscillations. Closure of the left mandible led to excitation of both the regular brief bursts and the intermittent longer bursts from larger units (Figure 28e). That is, contralateral afference from the left mandible has both excitatory and inhibitory directionally-sensitive influences on different right VMRO units during imposed movement of the left mandible.

The origin of the contralateral afference was shown to be partially from the left VMRO. Figure 31 shows the responses of the right VMRO to a series of imposed mandible oscillations. Oscillation of the right mandible shows the inhibitory effect of closure on the VMRO. Responses were recorded at both extremes of position but most units were silent during closing (Figure 31a). Similar oscillations of the left mandible resulted in a minimum of activity with the left mandible open (Figure 31b). Essentially the same pattern was obtained after dissection of the left mandible to expose

Figure 28

Records made from the sensory nerve from the ventral muscle receptor organ in the right mandible. The mandibles were moved passively. All nerves were intact. Upper trace monitors mandible position in b-e.

(a) Mandible closed to contact with left mandible. Reference position, 0^{o}.

(b) 16^{o} open from reference position.

(c) Response to imposed mandible opening. Sustained activity at positions 16^{o}, 20^{o}, 23^{o}, 27^{o}. Excerpts from a continuous recording where position was changed during an interval of 2-3 seconds.

(d) Progressive opening of the left mandible while recording from the right mandible held 23^{o} from open. Left mandible positions 0^{o}, 10^{o}, 17^{o}, 22^{o}.

(e) Left mandible closure from 22^{o} to 5^{o}. Right mandible held 23^{o} open. This trace is a continuation of those in part d.

(Timebase 21mm/sec on original.) The gain in (a) is higher than in (b-e) where it is constant. The arrow denotes direction of closure of the manipulated mandible.

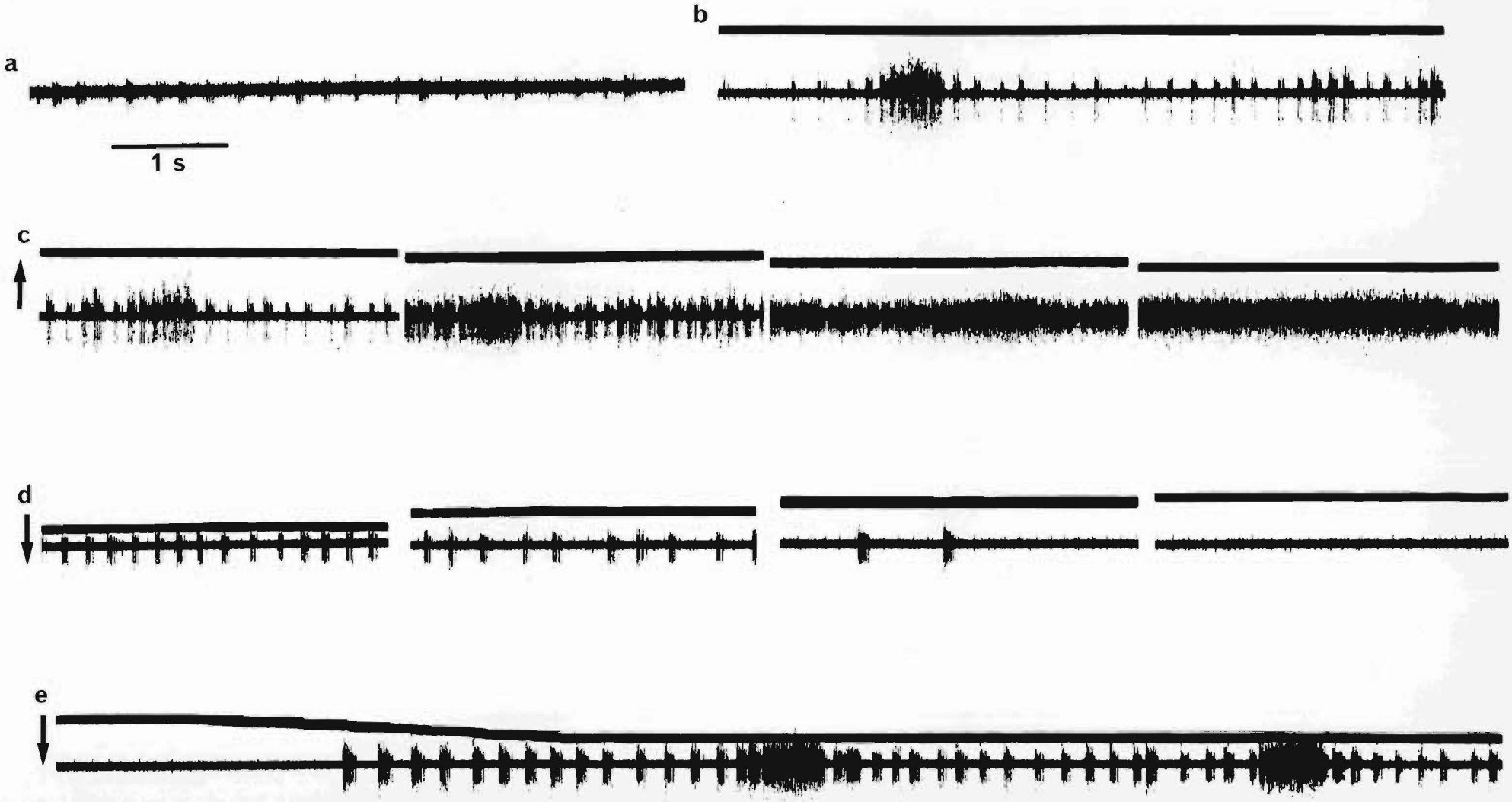

a
b
1 s
c
d
e

Figure 29

Extracellular recordings of sensory activity from the dorsal and ventral muscle receptor organs.

(a) Ongoing activity recorded from the right VMRO sensory nerve with a pin electrode while the mandible was held in a fixed position. The four traces are sequential sections of one recording.

Calibration 1.0s.

(b) Simultaneous extracellular recordings from the right VMRO sensory nerve (upper) trace and muscle TM-2a (lower trace) with the mandible held in a fixed position.

Calibration 1.0s.

(c) Hook electrode recording from the right DMRO sensory nerve with -

[i] ongoing activity

[ii] increasing activity during imposed mandibular opening

[iii] decreasing activity during imposed mandibular closure

[iv] phasic responses to tapping the sensory muscle lightly

[v] repeat of trace iv

[vi] increased discharge following stroking of head capsule with paintbrush.

Calibration 0.2s.

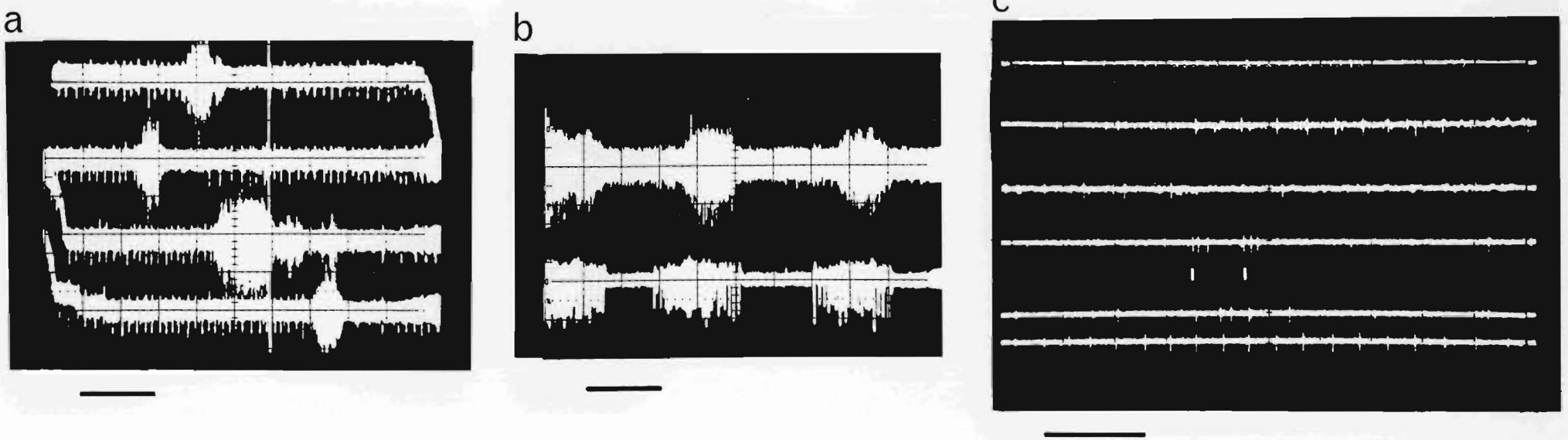

a
b
c

Figure 30

Hook electrode recording from the ventral muscle receptor organ in the right mandible during passive movement of the mandible. Both circum-oesophageal connectives have been cut, as well as nerve II in the right mandible. The larger units in each trace have been retouched.

(a) Mandible in positions 0^{o}, 13^{o}, 26^{o}, 11^{o}, 0^{o} open from rest.

Vertical calibration 20^{o}

(b) Following section of trunk I, which carries the motor nerves to the VMRO. Right mandible moved through 20^{o} from rest (0^{o}) and back to 6^{o}.

Vertical calibration 20^{o}

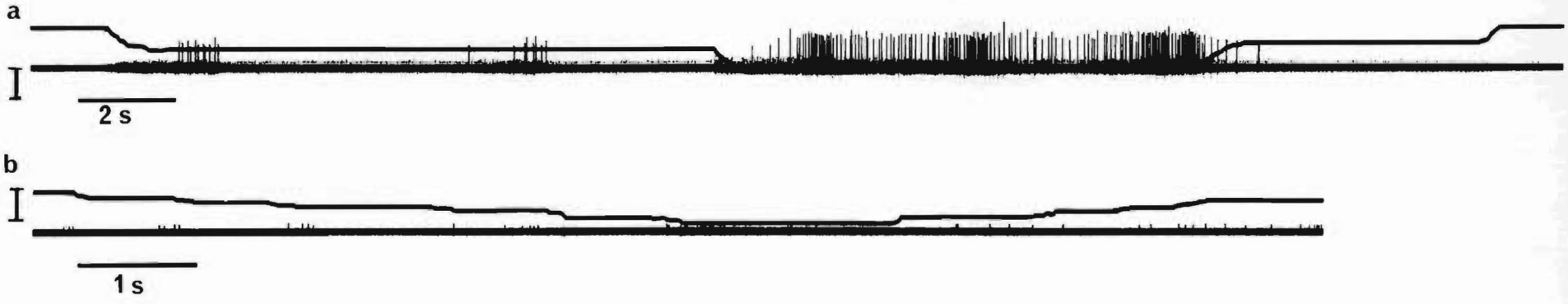

a
2 s
b
1 s

Figure 31

The influence of ipsi- and contralateral imposed mandibular displacement on the discharge of the right VMRO, recorded with extracellular hooks on the sensory nerve.

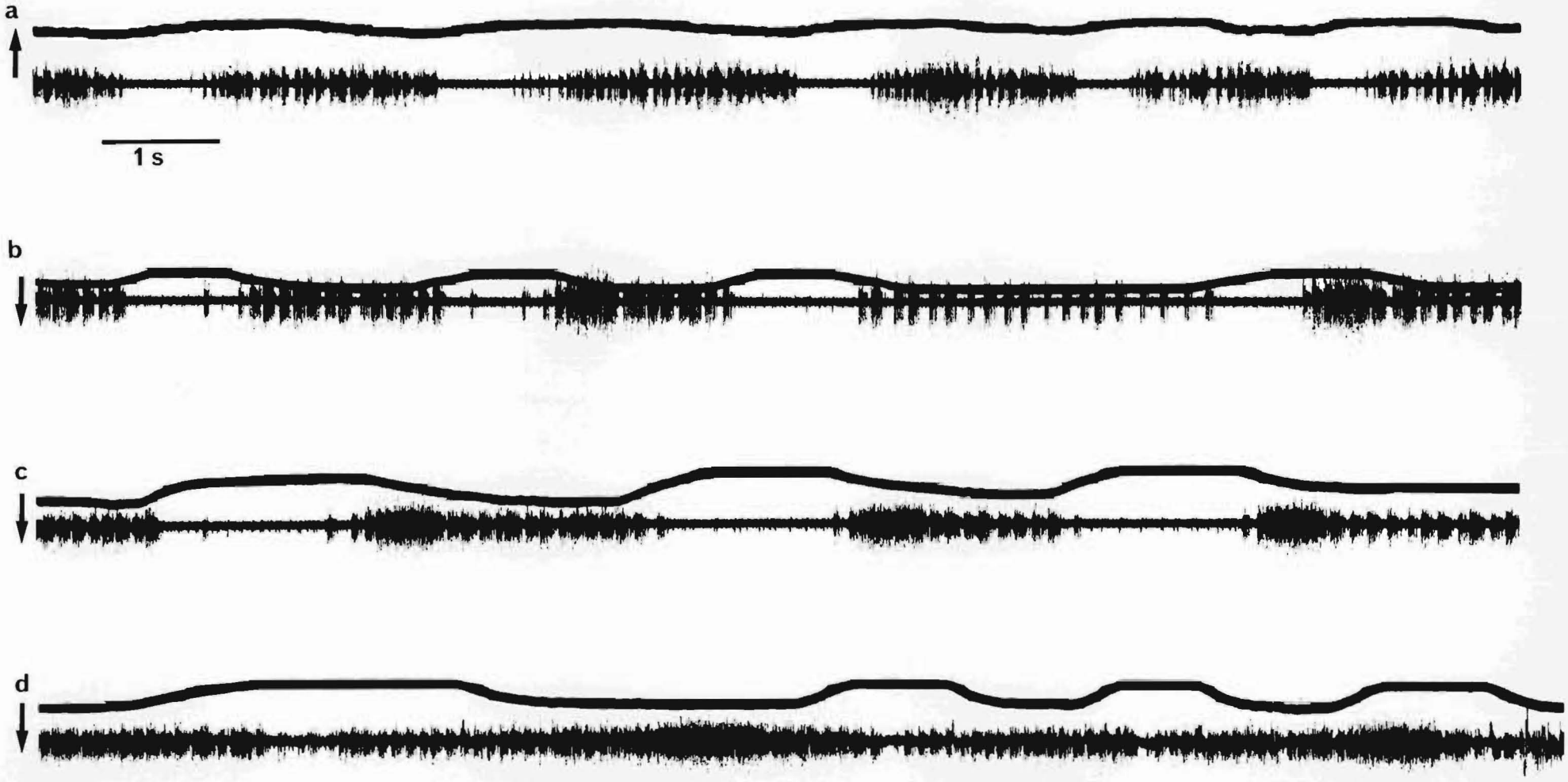
In all traces the arrow indicates the direction of adduction (closure).

(a) Imposed oscillation of the right mandible.

(b) Imposed oscillation of the left mandible prior to any dissection.

(c) Imposed oscillation of the left mandible after dissection to expose the sensory nerve of the left VMRO.

(d) Imposed oscillation of the left mandible after cutting the left VMRO sensory nerve close to the sense organ.


a
1 s
b
c
d

the sensory nerve from the left VMRO (Figure 31c). The phasic bursts from larger units in these two traces appeared to be in phase with left mandible closure, although one occurred with the left mandible open and they were not present in all cycles. In this animal the bursts occurred any time after a stationary 'left-open' position was reached until the next opening movement had begun. Most commonly they were in phase with left mandible closure if they were present at all. Cutting the sensory nerve from the left substantially reduces inhibition of the right during passive left mandible opening (Figure 31d) although a weak inhibitory influence was still evident. All semblance of a consistent phase relationship between left mandible position and the discharge of the largest units was lost, the final cycle even showing a burst during opening.

II THE DORSAL MUSCLE RECEPTOR ORGAN AND MINOR SENSE ORGANS

(1) The anatomy of the dorsal muscle receptor organ

The dorsal muscle receptor organ, DMRO, is a simple structure consisting of a few muscle fibres, one motor neurone and a single primary receptor cell at the muscle insertion. The muscle is exceedingly slender, with a cross-sectional area of less than 0.02 square millimetres. Together with its unusual origin this suggests that the muscle is incapable of contributing significantly to the force of adduction. The receptor muscle is muscle TM-2b which arises from the 2a branch a short distance from its attachment to the tentorium (Figure 32). In

some specimens there appeared to be a short 2b apodeme which fused with the connective tissue forming part of the attachment of 2a to the tentorium. In other preparations this was less evident and the muscle fibres of the two branches appeared to merge and run in parallel toward the tentorium. In no case did TM-2b arise directly from the tentorium. The insertion is on the dorsal wall of the mandible about 2mm from its basal margin. The muscle is therefore about $2\frac{1}{2}$mm long in a mature male with the mandible in the rest position. It lies almost parallel to the mandibular cuticle and in some fixed preparations the muscle curved slightly as it passed under the basal margin of the mandible.

Mean sarcomere lengths ranged from 4.1-6.2µm in fibres where at least 10 adjacent sarcomeres could be counted. The range for muscle TM-2a fixed in situ with alcoholic Bouin's in the same mandibular position was 5.4-11.6µm. In several preparations the mean sarcomere length for TM-2b was less than half that of TM-2a.

The single motor neurone leaves the suboesophageal ganglion in trunk III and, together with the hypopharyngeal retractor motor neurones, leaves this trunk via the proximal arm of the branch carrying dendritic process of the apodeme strand receptor (Figures 32, 34d). It is carried in the receptor strand to where this connects with muscle TM-2 and then passes along the ventral side of the receptor muscle, often in a slight groove.

The axon of the single sensory cell is carried in trunk II, the nerve containing the abductor motor

neurones. The first branch of this trunk carries sensory axons from the dorsal mandibular cuticle, including the DMRO axon (Figure 32). The primary cell body is found immediately adjacent to the distal end of the receptor muscle on the same side as the nerve. It is not attached to the muscle.

Shortly after leaving the soma the dendrite divides (Figure 34b) and dendritic branches enter the collagenous connective tissue matrix between the terminal portions of the muscle fibres and the hypodermis (Figure 33a,b). Finer dendritic processes containing mitochondria and microtubules can be seen ramifying throughout this collagen-like tissue (Figure 33d). Often the dendritic process may be accompanied by glial cells (Figure 33b,d) but no dendritic processes have ever been observed to enter the muscle fibres.

The muscle fibres resemble those of the other skeletal muscles rather than the fibres of the VMRO. In transverse section they are compact, more or less regular polygons about 5-7μm across (Figure 34e). Virtually all the cross section is occupied by filaments grouped into rather irregular fibrils up to 1μm across. The fibrils are not arranged in any obvious pattern. Nuclei are peripheral and tracheal development is poor. The mitochondria are up to 1.2μm long and are longitudinally aligned amongst the fibrils. The Z-discs of adjacent fibrils are closely in register (Figure 34c). Sarcomere lengths of 4.1-6.5μm have been recorded from muscle fixed in situ in alcoholic Bouin's.

Figure 32

Nerve and muscle anatomy of the mandible revealed by frontal dissection.

'a' - Nerve branch to the cuticle in the region of the anterior articulation.

'b' - Nerve containing the axons from the campaniform sensilla adjacent to the anterior articulation.

'c' - Nerve supplying the lateral wall of the mandible near the M-26 insertion.

'd' - Nerve supplying the cuticle near to the DMRO insertion.

'e' - Nerve containing the axons from the cusp receptors and more distal regions of the mandible.

mn to TM-2b - motor neurones to the dorsal receptor muscle and to muscle TM-2b; rs - apodeme receptor strand; sog - suboesophageal ganglion; II, III - mandibular nerve trunks; VMRO - ventral muscle receptor organ.

Inset top left: the region of dissection.

Inset top right: detail of the origins of the dorsal receptor muscle (TM-2b) on muscle TM-2a.

Inset bottom left: stylised diagram of the insertion of the dorsal receptor muscle showing the nerve containing the sensory axon, and nerve 'd'.

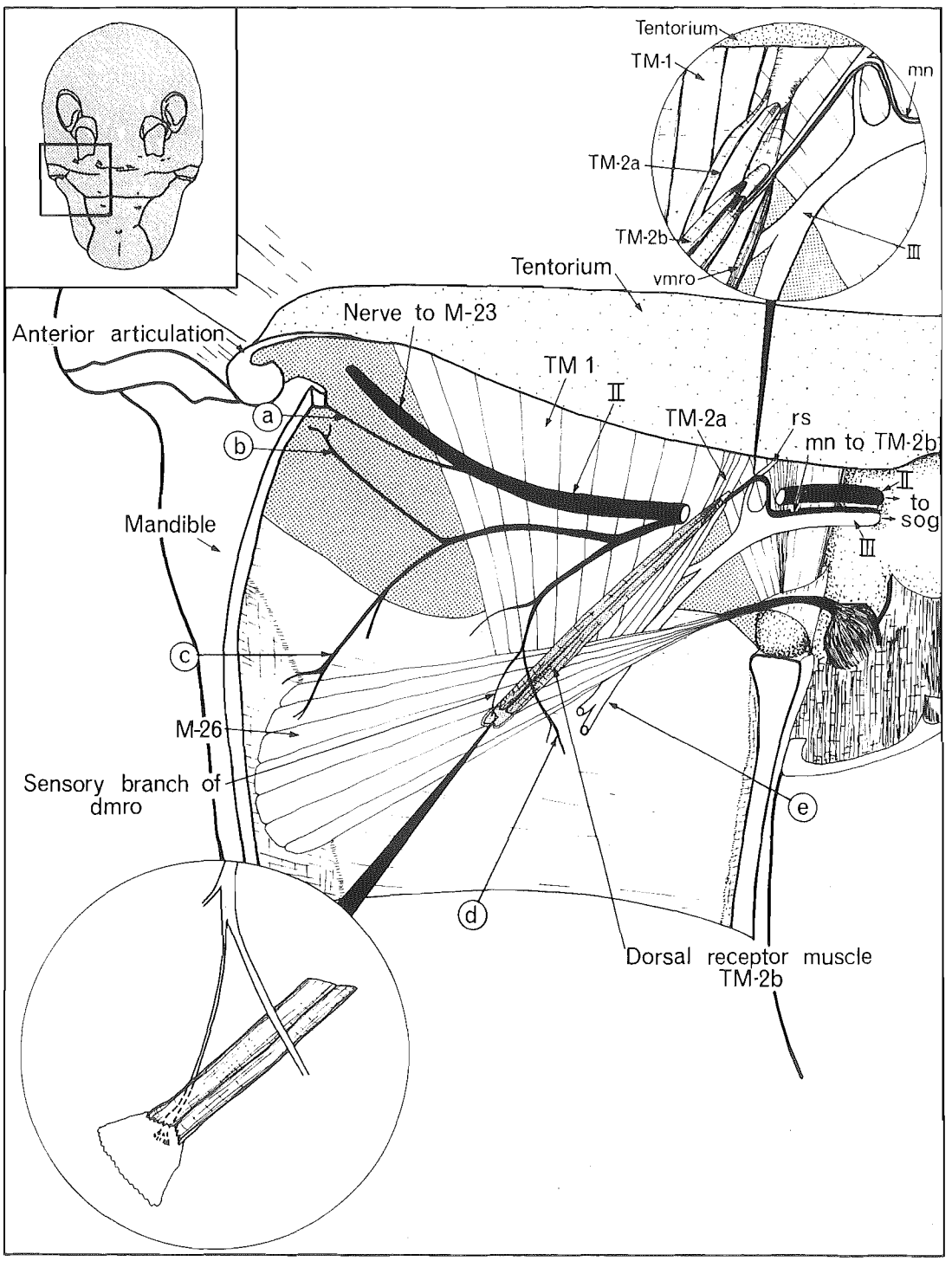

Tentorium
TM-1
mn
TM-2a
TM-2b
III
vmro
Tentorium
Anterior articulation
Nerve to M-23
TM 1
II
TM-2a
rs
mn to TM-2b
II
to sog
III
a
b
Mandible
c
M-26
Sensory branch of dmro
e
d
Dorsal receptor muscle TM-2b

Figure 33

Ultrastructure of the dorsal muscle receptor organ.

(a) Fibrous material with collagen-like banding. Higher-power detail of the substance in which the sensory dendrites are buried.

Calibration 0.2μm

(b) Terminal region of the muscle receptor organ showing muscle fibre endings (mf). Dendritic profiles (dd) surrounded by glial cells (gl) are embedded in the fibrous connective tissue matrix (mx) which contains dense tracts of fibres oriented in parallel (ft). Cells forming a hypodermal region (h) border the connective tissue matrix on the left.

Calibration 2μm

(c) Higher power view of the receptor muscle fibres (rm) ending in the connective tissue matrix (mx). Thick filaments (f) are seen in longitudinal section in the muscle.

Calibration 1μm

(d) Dendritic profiles containing neurotubules (arrowed) and mitochondria penetrate the connective tissue matrix. The dendrites here are surrounded by a single layer of glial cells (gl).

Calibration 1μm

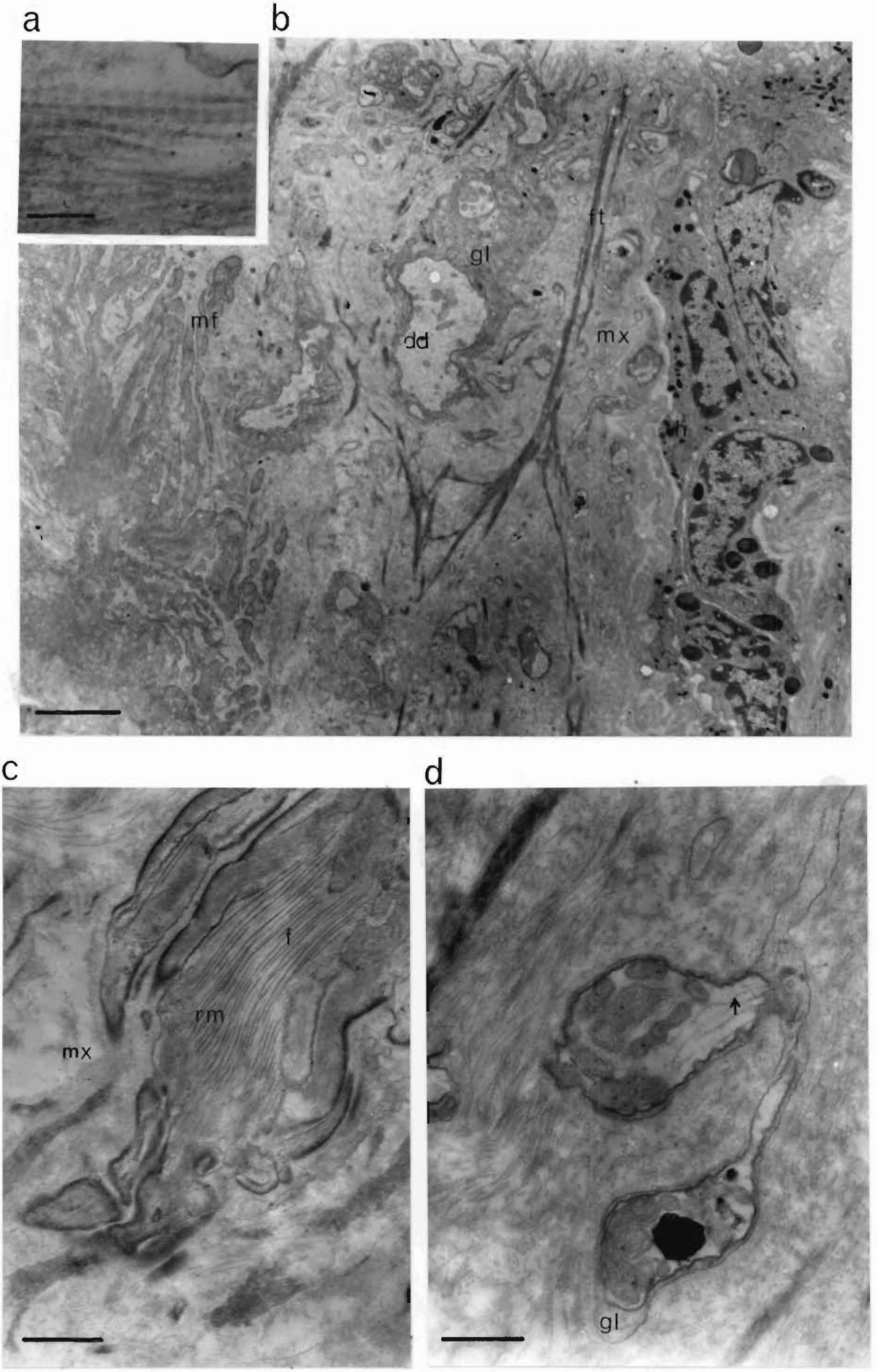

a
b
mf
dd
gl
ft
mx
c
mx
rm
f
d
gl

Figure 34

Ultrastructure of the dorsal muscle receptor and the apodeme strand receptor.

(a) Sensory cell body from the group innervating the apodeme strand receptor. Sensory axon profiles from nerve trunk III are visible.

Calibration 3μm

(b) Transverse section through the dendritic processes of the single sensory cell of the dorsal muscle receptor organ. The section is very close to the cell soma. The dendrites are surrounded by glial cells (gl). The dendrites are quite separate from the receptor muscle (rm) at this level.

Calibration 1μm

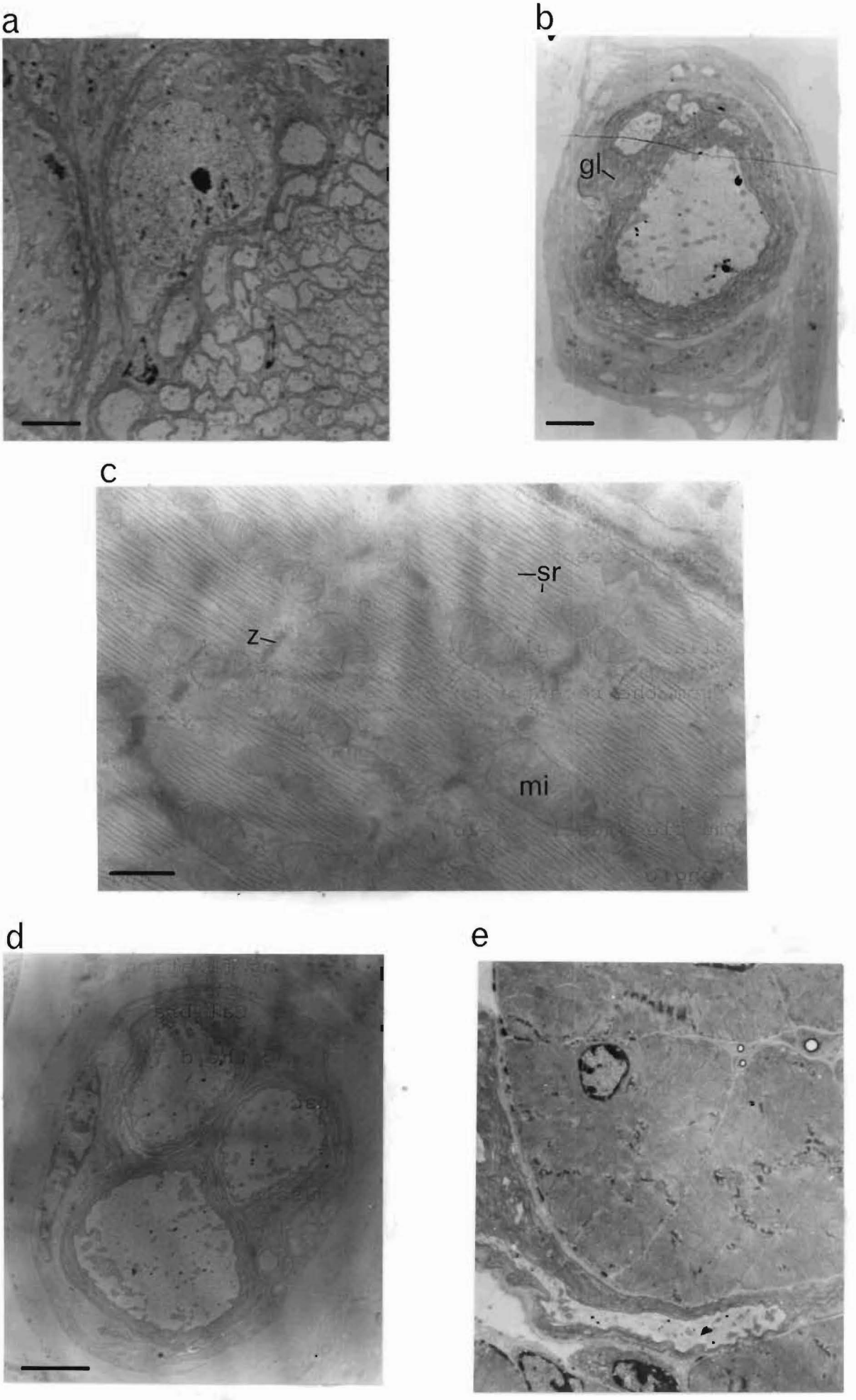
(c) Longitudinal section of the receptor muscle (muscle TM-2b), showing Z-discs (z), longitudinally-oriented mitochondria (mi) and sarcoplasmic reticulum (sr). The short sarcomere length is due to contraction during fixation.

Calibration 0.5μm

(d) The motor nerve supplying the dorsal receptor muscle (TM-2b) and muscle M-26, which retracts the hypopharynx. The section is taken where the nerve runs beneath muscle TM-2b, after it leaves the receptor strand and before the two axons to muscle M-26 branch off.

Calibration 2μm

(e) Transverse section of a muscle fibre from the dorsal receptor muscle (TM-2b).


a
b
gl
c
sr
z
mi
d
e

(2) Physiology of the DMRO

The observations presented here are derived from two preparations only. Extracellular recording from the sensory nerve with the mandible held in a partly open position revealed a low level of ongoing activity, which increased in response to imposed mandibular opening, and decreased on closure. Both stretching the receptor muscle along its axis and deflecting it slightly elicited phasic increases in activity. These stimuli may have been outside the normal range. Taking values assessed for other insects, the maximum force exerted by a muscle as slender as TM-2b is likely to be less than 1gm. Disturbance to the preparation, as in stroking the head capsule with a paintbrush, sometimes elicited changes to the resting level of discharge. Most of these points are illustrated in Figure 29c. Pressure on the cuticle near to the receptor muscle insertion inhibited ongoing activity. Cutting the receptor muscle reduced the discharge rate, to zero in one case, but this later recovered partially. Cuticular pressure continued to inhibit the discharge following muscle transection. It is not known if cuticular distortion is a natural stimulus in the intact animal.

(3) Apodeme strand receptor

Associated with the tentoro-mandibular muscle complex is a third strand receptor spanning the mandibular joint. A thin, transparent flexible strip of cuticle leaves the surface of the apodeme of the

main adductor muscle (M-21) (Figure 24). It attaches, as a slightly thickened opaque strand, to muscle TM-2 at the junction of the "a" and "b" branches. The change in appearance is due to neural tissue which is found from approximately the position where the strand passes under the largest nerve trunk to muscle M-21. The very flexible portion arising from the M-21 apodeme is inelastic and appears not to include any neural tissue. Therefore any stretch applied to the receptor will not be distributed along its entire length. While one end of the receptor attaches to the TM-2 muscles, the area of attachment is close to the tentorium allowing little movement. The major changes in receptor length arise from movement of the M-21 apodeme. The receptor is stretched during adduction, or closure. The length may decrease to less than half the resting length during a 40^{o} mandibular excursion. As the physiology of this receptor has not been investigated the possibility of stimulation arising from activity in muscle TM-2 cannot be excluded.

The sensory cell bodies are not found on the receptor strand. Approximately 24 cell bodies are aggregated in a compact cluster protruding from the margin of nerve trunk III. Most commonly this is found where the nerve passes over the M-21 apodeme and connects to the receptor strand via two fine processes of approximately equal dimensions (Figure 24). Variations on this pattern included greater development of the proximal process and finer branching of either process before connexion with the receptor strand. Methylene

blue preparations revealed fine processes passing into the connective tissue between the processes linking the cell bodies and strand. Rarely, the cell body grouping, or pseudoganglion, is situated much closer to the suboesophageal ganglion and a single long process connects it to the receptor strand.

The group of cell bodies is simply that. No synapses were seen within the grouping using the electron microscope. The sensory cell bodies appear similar to those of the ventral muscle receptor organ (Figure 34a). Their axons are found along the same margin of nerve trunk III as the cell bodies.

Intimately associated with this receptor are the motor axons to the hypopharyngeal adductor muscle and muscle TM-2b. These also leave the suboesophageal ganglion in nerve trunk III and pass into the receptor strand by way of the proximal process from the sensory cell body group. The three axons leave the receptor strand and continue along the same axis on the ventral side of muscle TM-2b (Figure 32). Under the dissecting microscope it was not possible to determine where the receptor portion of the strand finished, or precisely where it was attached to the muscle.

(4) Campaniform sensilla

Several groups of campaniform sensilla are found on the mandibles. The most obvious of these, referred to as the ventral group, lies in a distinctly differentiated region of cuticle on the ventral surface of the mandible between the insertion of the TM-1 muscle

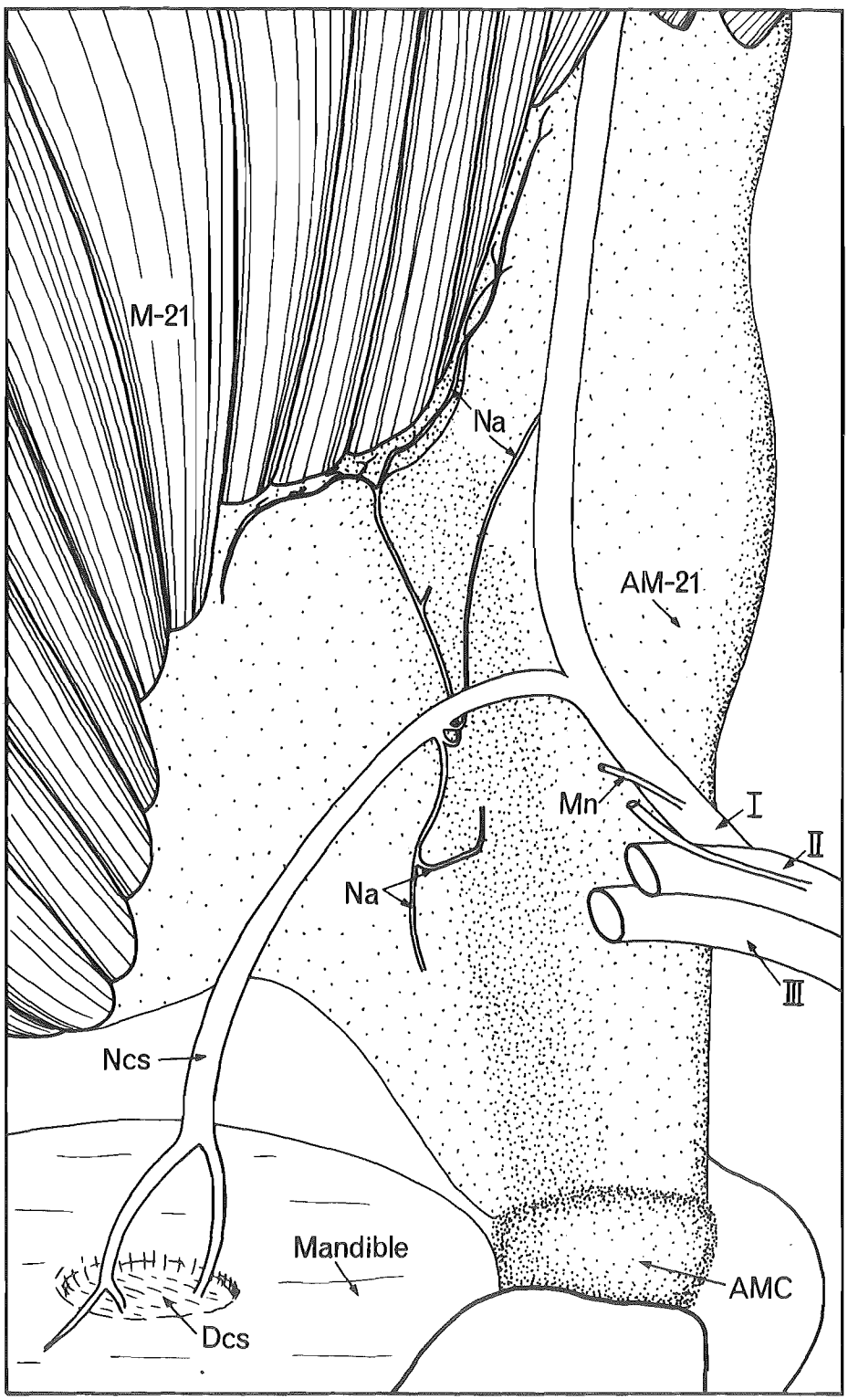
and the basal margin of the mandible (Figure 36a). Here the cuticle is thinner and less heavily tanned than in the immediately surrounding region. The thinned area is slightly recessed and developed into several folds which lie approximately parallel to the basal margin of the mandible. This specialised region of cuticle lies almost on the axis between the mandibular hinge line and the insertion of the major adductor apodeme.

Within the ridged area lie 12-20 campaniform sensilla with their longer axes oriented in parallel with the cuticular folds (Figures 36c). In some animals the folds are less pronounced although the cuticle is still thinned and recessed slightly. In this situation the same orientation of the sensilla is found, all being oriented with their long axes across the long axis of the mandible. As the sensilla are approximately halfway between the hinge line and the point of force application (the adductor apodeme) it is difficult to estimate the direction of stress they would be exposed to. Their proximity to the TM muscle insertions complicates this. A few sensilla lie even closer to the TM insertion than the grooved region of cuticle. These lie close to, but outside, the area of thinned cuticle. All are innervated by the same nerve, a branch of nerve trunk I which also contains nerves innervating the M-21 apodeme (Figure 35). Two fine branches supply the ridged area of the cuticle, which appears from inside the mandible as a depression where the cuticle is thinned. One of these branches

Figure 35

Nerve supply to the ventral group of campaniform sensilla and to the principal adductor apodeme.

AM-21 - apodeme of adductor muscle M-21; AMC - flexible region of the adductor muscle apodeme connecting it to the mandible; Dcs - depression on the internal surface of the mandibular cuticle corresponding to the thinned cuticle beneath the ventral group of campaniform sensilla; M-21 - the principal adductor muscle; Mn - motor nerve supplying muscles TM-1, TM-2a and the VMRO; Na - the fine sensory nerves ending on the M-21 apodeme; I, II, III - the major mandibular nerve trunks.


M-21
Na
AM-21
Mn
I
II
III
Na
Ncs
Mandible
AMC
Dcs

supplies the surrounding cuticle from a finer branch immediately before the cuticular depression is reached.

Two other groups of campaniform sensilla are associated with the two articulations. Neither is in an area of differentiated cuticle, and the sensilla are not grouped into a small area.

The sensilla on the frontal surface of the mandible near the anterior articulation are innervated by a branch from nerve trunk II (Figure 32). Excitatory responses have been recorded during mandibular adduction.

Campaniform sensilla have also been found adjacent to the base of the "ball" part of the posterior articulation.

(5) The cusp receptors

The more distal regions of the mandibular cuticle, including the entire cusp region, are innervated by the distal portion of nerve trunk III. A cross section of this trunk taken just distal to the departure of the VMRO branch revealed approximately 2,700 axon profiles. These ranged in size from 0.3μm to 2.5μm. Both dissection of the nerve trunks (Figure 37) and peripheral filling of these trunks with cobalt chloride revealed a rich innervation of the entire cusp region (that is, the heavily sclerotised cuticle in the region of mandibular occlusion). The details of sensory structure were not examined further save that no sensilla were found on the external surface of

the cuticle.

Recordings were made from the nerves from the cusp region using paired silver hooks. The signals were very small and often not clearly discernible from the amplifier noise on the oscilloscope screen. However, clear responses could be distinguished when the signal was fed into an audiomonitor. No unit monitored had a resting discharge when unstimulated. Light touch with a hand held glass probe elicited phasic responses upon initial contact and when the probe was removed. It was not apparent whether the "on" and "off" responses came from the same or different units. Continuously applied pressure gave a maintained low-level discharge. Greater applied forces recruited more units. These may have been higher threshold units in the region of the probe or possibly more distant receptors responding to a more widely-spread cuticular distortion. The "off" responses may have resulted from small lateral movements of the probe as it was being released. That is, they may have been "on" responses elicited from previously unstimulated units.

(6) Hairs bordering the cusps

The sclerotised portions of the more proximal cusps are bounded by articulated hairs lying close to the cuticle with their tips directed toward the cusp margins (Figure 38a,c). On the inner margin of the mandible immediately proximal to the cusps is a denser aggregation of larger hairs known as the brush or brustium (Figure 38a,b). Although these are articulated,

Figure 36

Scanning electron micrographs of cuticular sensilla of the mandible.

(a) Ventral view of the basal region of the left mandible of a female weta. A group of simple articulated hairs is shown. The ventral group of campaniform sensilla (cs) is in the cuticular folds adjacent to the letters, and in the immediately surrounding cuticle. The other cuticular folds correspond to the insertions of muscles TM-1, TM-2a, and the VMRO.
aa - posterior articulaion.

X16

(b) Detail of the hairs shown in 'a'.

X300

(c) Detail of the cuticular folds of the ventral group of campaniform sensilla. The long axes of the sensilla are parallel to the folds.

X570

(d) Higher power view of the campaniform sensilla.

X870

(e) Shorter sensilla found near the anterior articulation and carina of the mandible.

X430

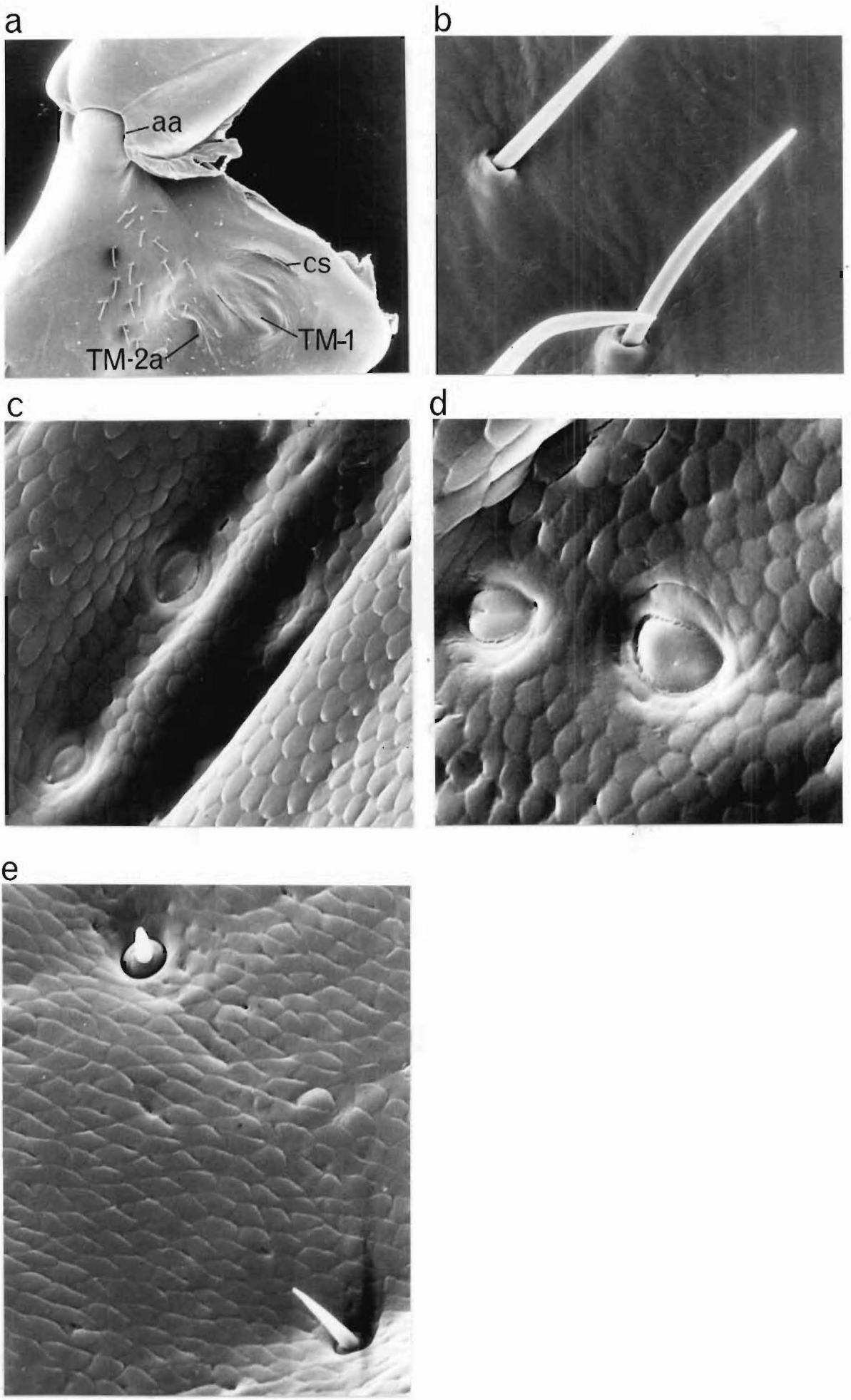

a
aa
cs
TM-1
TM-2a
b
c
d
e

Figure 37

The innervation of the more distal parts of the mandibular cuticle.

The nerves shown all converge into a single nerve which then joins the VMRO sensory nerve to form the bulk of nerve trunk III. Lb denotes a branch innervating the distal parts of the carina and fronto-lateral areas of the mandible. All other branches terminate in the cusp regions.

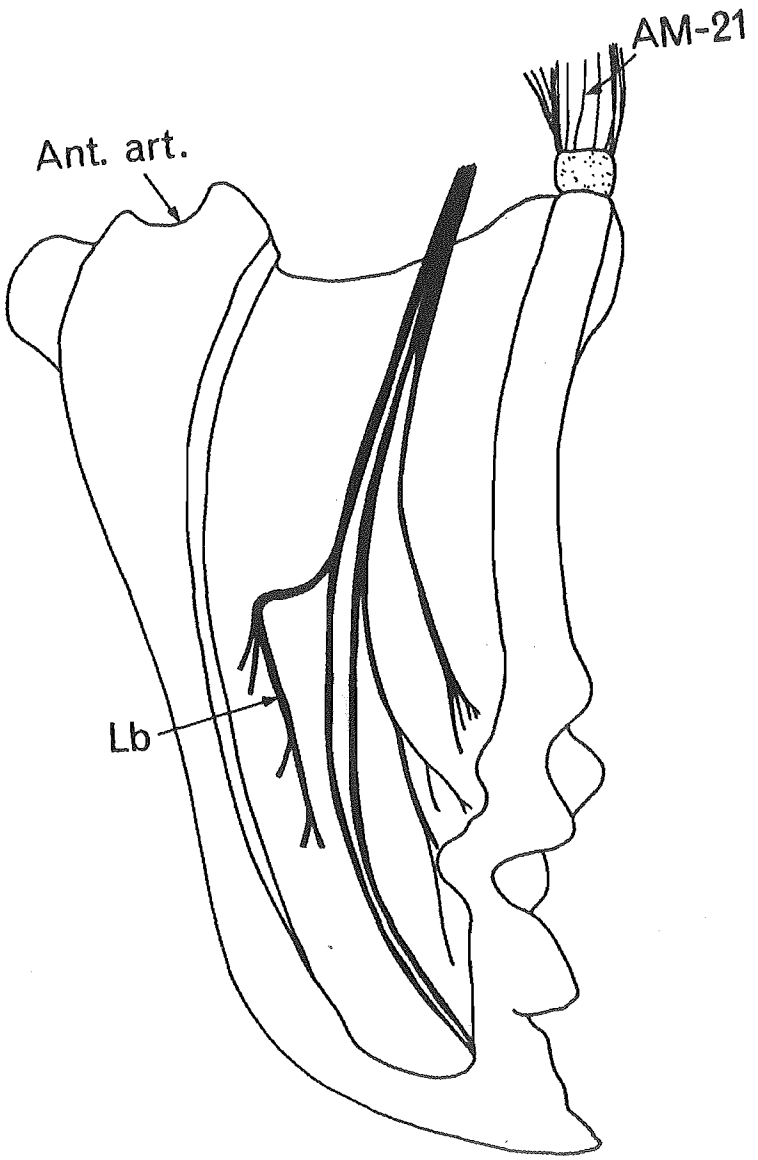

AM-21
Ant. art.
Lb

Figure 38

Hairs and sensilla associated with the mandibular cusps.

(a) The cusp region of the right mandible of a male weta, showing the brush region (b) proximal to the cusps.

X11

(b) Detail of the longer hairs found in the brush region and around the bases of the cusps.

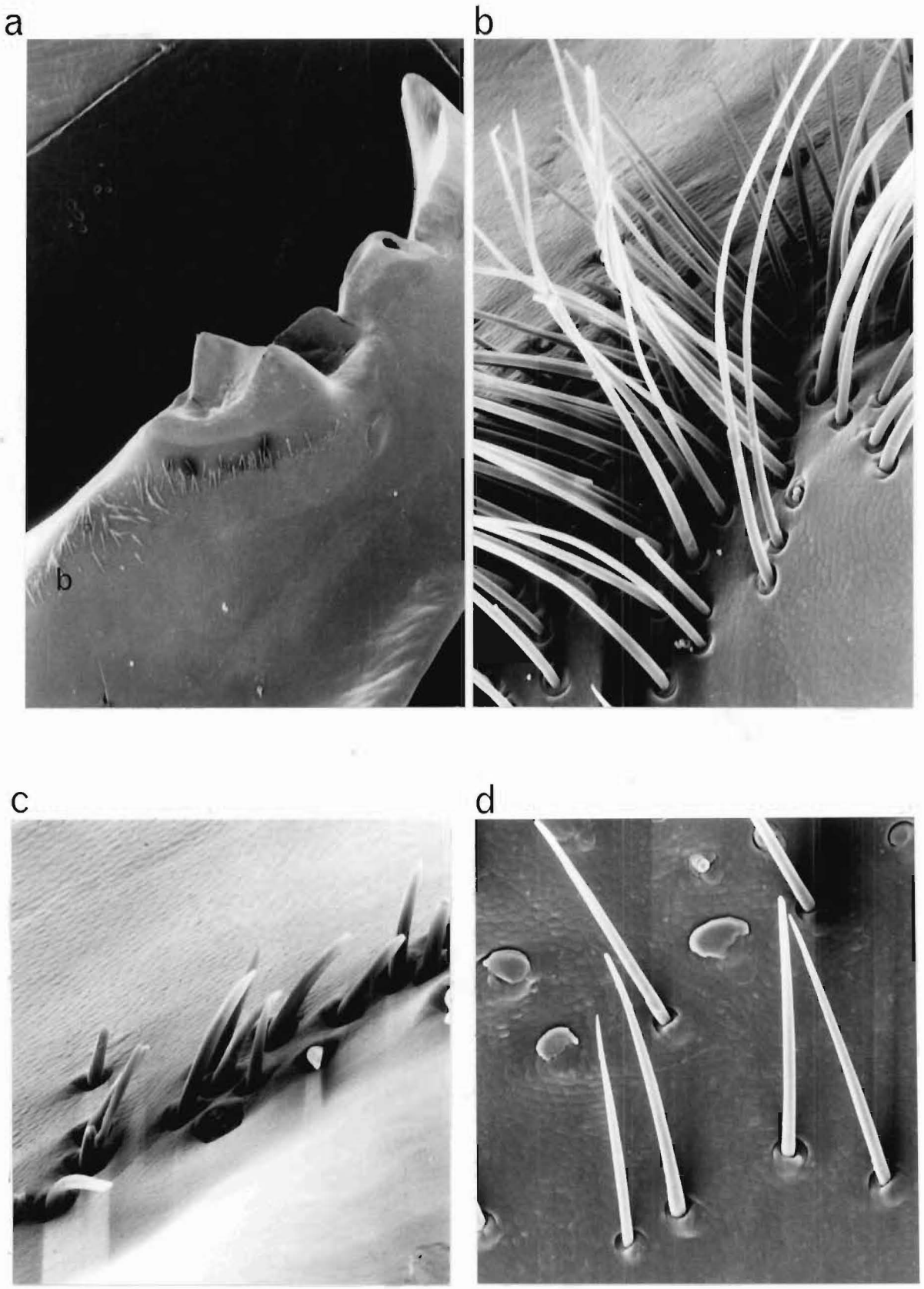
X180

(c) Shorter hairs found adjacent to the cusp bases.

X220

(d) Longer hairs, probably innervated, found near to the cusp region.

X190


a
b
b
c
d

they have no nerve supply that could be detected during dissection.

(7) Cuticular sensilla on the mandible

There is a sparse distribution of various sensilla types over much of the mandible. A denser grouping of setae more than 200µm long is found on the ventral surface of the mandible in the region between the TM-1 muscle insertion and the posterior articulation (Figure 36a,b). These setae are also found in lesser numbers on the ventro-lateral regions of the mandible. Similar setae (Figure 38d) are found near to the cusp bases on the frontal parts of the mandible. These appear to correspond to the type 1 sensilla described from Schistocerca (Thomas, 1965).

Also on the frontal part of the mandible in the sclerotised regions near the carina are much shorter, peg-like sensilla found in recesses in the cuticle (Figure 36e). These resemble the type 2 sensilla of Thomas.

The pattern of nerve branching to the mandibular cuticle is shown in Figures 32 and 37. The pattern of branching in the more proximal parts of the nerve joining trunk III can vary considerably.

(8) Innervation of the adductor apodeme

Cobalt chloride filling of the peripheral portions of nerve trunk I has revealed several fine nerve branches passing into the connective tissue covering the apodeme of the principal adductor muscle, M-21

(Figure 35). These three nerves leave the branch to the campaniform sensilla shortly after it separates from the M-21 motor supply. One of the three fine branches runs toward the coupling of the apodeme to the mandible, before branching again. A second branch runs along the apodeme in the opposite direction. The terminations of these nerves are unknown. The third nerve runs along the border of the M-21 muscle fibre insertions onto the M-21 apodeme (Figure 35). Many fine branches are given off. These appear to penetrate the apodeme cuticle. In no case were they found to contact the muscle fibres. Further details of their endings are unknown.

(9) Other sites of sensory input

Suction electrode recording from the distal portion of nerve trunk II, revealed a single large unit phasically active during mandibular closure. Manipulation suggested that the receptor may be associated with the anterior articulation, in which case the axon would be found in the fine nerve branch labelled 'a' in Figure 32.

CHAPTER VII

THE ACTIVITY OF THE MANDIBLES AND THE INFLUENCE OF THE VMRO

In order to test the peripheral control mechanisms of the mandibles, either their movements or the forces they generated were monitored in several behaviours. Feeding and biting on a rubber tube were examined before and after ablation of the VMRO. This operation involved the detachment of the distal end of the receptor from its insertion onto the mandible, releasing it, with its neural connexions intact, into the body of the mandible. The procedure is described in Chapter II. The load-compensating capabilities were tested by adding weights to create constant forces in the direction of opening. The movements involved in the threat display and defensive biting were examined before concentrating on the forces generated in defensive biting. The effects of VMRO ablation on several parameters of the defensive bite were examined in detail. Possible influences from the campaniform sensilla and cusp receptors were also tested.

I ABLATION OF THE SENSE ORGANS

Post mortem examinations of each experimental animal after fixation in alcoholic Bouin's showed receptors shortened to 60-70% of the length they would assume in the intact animal. The fixation process may have contributed to the observed shortening. The receptors

were often curled and were seldom aligned along their usual axis. Sham operations in which a piece of cuticle was removed immediately adjacent to the VMRO insertion had no effect on any of the behaviours described below. Elongated hair sensilla (Figure 36a) were removed from the region of the insertion during the ablation. This had no discernible effect.

If the cuticle over the insertion was abraded but the receptor not cut free, it was found to shorten slightly but not detach from the surrounding tissue. In this condition no disruption of behaviour was apparent.

Elimination of the ventral campaniform sensilla could be readily confirmed under the dissecting microscope.

II MANDIBULAR MOVEMENTS IN FEEDING

Ablation of the VMRO can be shown to affect coordination during activities where the mandibles are completely unrestrained. This is evident in unrestrained defensive biting and in masticating food. As patterns of chewing alter with different types of food the data presented here relate mostly to feeding on apple, a potent feeding stimulus. Even unpalatable substances such as polystyrene would be chewed if apple juice was applied to the maxillary palps. Apple can be presented in pieces of varying sizes thus testing manipulative abilities more than would a flat piece of leaf. Finally, it can be bitten through and masticated with comparative ease, unlike more fibrous matter such as chicken, another readily accepted food. Chewing

patterns were examined in 14 animals.

Chewing begins with a series of ineffective mandibular closures which progressively increase in amplitude until a functional sequence is developed by the fourth or fifth cycle. Shorter initiation phases may occur, particularly after other feeding or biting sequences. The morphological asymmetry of the mandibles is reflected in markedly different movement patterns of the two mandibles (Figure 39). The longer, overlapping left mandible reaches the open position of each bite closely in phase with the right. It then closes more or less smoothly and evenly until it has assumed approximately its normal rest position. When inactive the mandibles are held in close apposition with the terminal cusps overlapping.

At this stage the right mandible is well short of its normal resting position but contact may be made at the terminal cusps and there may be resistance developed as the food is compressed. These factors are reflected in irregularities in the closure phase of the right positional trace.

While the right mandible is still closing, the left remains in approximately the same position. During regular chewing the fully closed position may be maintained for up to 45% of the total duration of any cycle, often persisting until after the right mandible has begun to open (Figure 39a). A feature of the "plateau" phase is deflection of the left mandible by the right in the fully closed position. This is represented by a very slight depression in the

left trace near the middle of the plateau region. While the deflection is slight it is clearly visible in all chewing animals. The basic pattern of mastication is then for the left mandible to close before the right, reaching its fully closed position perhaps 0.2-0.3 secs earlier in a cycle lasting 1.5 seconds. The right then completes its closure, deflecting the left slightly, and begins to open before the left. Once contact between the mandibles has been lost, the left also opens and peak opening position is reached closely in phase with the right. Such a pattern may persist for several minutes usually at a frequency of 0.8-1.0Hz when chewing a small bolus of fibrous material. Sustained mastication is rarely much faster than 1Hz and may be rather slower, down to 0.6Hz in some animals. The frequency here reflects the motivational state of the animal rather than the texture of the food.

Other properties of the food contribute to the observed pattern. The trace in Figure 39b shows feeding on a piece of apple too large to be fully contained within the mouthparts. The excursion of each mandible is clearly greater than during mastication of a small bolus, as shown at a later stage of the next trace (Figure 39c). As the gape increases the frequency drops, to less than 0.5Hz in this example. Clearly the frequency of oscillation can vary with the nature of the task. The maximum rates were recorded during feeding on Tenebrio larvae. Average frequencies of 2.3Hz were reached in burst of 3-4 cycles. Some instantaneous frequencies exceeded 3.0Hz but coordination

was poor in these instances, the duration of a bite cycle often differing between the two mandibles. The slowest rates of continuous oscillation were obtained during chewing on a compressible rubber tube 5.75mm in diameter. Such a tube placed between the gaped mandibles elicited prolonged bouts of regular but slow chewing movements. In one animal these averaged 0.21Hz over a series of 30 cycles.

The regular cycle of mastication can be interrupted by bites of longer duration. Figure 39b shows a wide gape, with superimposed weak closure movements, produced in biting into a piece of apple too large to be held in the mouthparts. This is followed by a prolonged closure bite of different form, principally used in shearing off portions of food. The left mandible moves much as in mastication but the plateau phase is greatly prolonged, to almost 2 seconds in this instance. The right mandible produces a more extreme closure of up to 10° greater excursion than in mastication. This biting off manoeuvre is usually interposed in a mastication sequence, occupying up to twice the normal cycle period.

The effects of VMRO ablation on mandibular coordination during feeding can now be examined.

Figure 39d shows a further sequence of apple-chewing following ablation of the right VMRO. The general bite form is not noticeably different and temporal coordination between the two sides is well maintained. Clearly the frequency has altered little, typifying the results found in other experiments. For

a brief portion of the middle of the trace the frequency rises above 1Hz, corresponding to a sequence of low amplitude bites. Right mandible excursion has decreased substantially relative to the left. Calculating the ratio of right to left (using mm deflection on the trace as the statistic) gives a mean of 1.1 for a sequence of 11 bites on the trace in Figure 39b. The same calculation for a 17-bite sequence in Figure 39c gives a mean ratio of 0.55 (U = 0, differences significant at the 1% level). As the initial ratios are partially a function of the gain of the recording system (see Methods section) they do not reflect the amplitude of left and right mandibles exactly. However the right/left ratio is a sensitive indicator of relative mandibular excursion within any given experiment. Here the ratio not only dropped in the post-operative trial, it also varied more, even for the larger amplitude bites. Despite this the pattern of decreasing and increasing amplitude in the left mandible is usually reflected in a similar change in the right.

Following ablation of the left VMRO the amplitude imbalance is rectified and perhaps overcompensated. The short section of trace in Figure 39c suggests that the new right/left amplitude ratio is greater than in the intact animal. For this short sequence R/L = 1.5, a value that is achieved through a high proportion of extreme "shearing-off"-type closures resulting in wide right mandible excursions, well past the "rest" position. The second trace in Figure 39e illustrates another alteration in coordination. In certain bites, indicated

by arrows, small right mandible bites are paired with large excursions of the left mandible. Here the left mandible has closed well past its normal position, preventing the appropriate matching with the right. The mandible tips meet briefly, giving an incomplete closure and then open. In the intervening bites, at first site more regular in form, there is further evidence of disrupted coordination in the pronounced inflexion of the left trace as the "closed" position is approached. A corresponding shoulder in the right trace is present in some instances, although it is not unique to the bilaterally-operated condition (see Figure 39c). These difficulties in coordination are even more apparent when the animal is observed than they are on the traces. Single ablations may cause more frequent mismatching than bilateral ones, presumably because the VMRO continues to discharge after the operation. Each ablation had slightly different effects.

III CHEWING OR BITING ON A RUBBER TUBE

Because the inconsistency of the behaviour gave poor base data against which to compare ablations, these experiments were limited to five animals.

Insertion of a 5.75mm diameter rubber tube between the mandibles elicited cyclical mandibular movements reminiscent of chewing. Apple juice applied to the tube and to the maxillary palps promoted this. The air-filled sealed tube presents a different set of

Figure 39

Mandibular movements before and after VMRO ablation during feeding on apple.

The right mandible is the upper trace of each pair. Closure is toward the midline.

(a) Masticating apple.

Calibration 1 second

(b) Biting into a piece of apple too large to be held completely within the mouthparts. A biting-off manoeuvre is shown (arrow). The horizontal trace preceding the biting sequence indicates the rest positions of the two mandibles.

Calibration 5 seconds

(c) Biting off and mastication of apple. Mastication of a small bolus held within the mouthparts is shown in the sequence following the arrow.

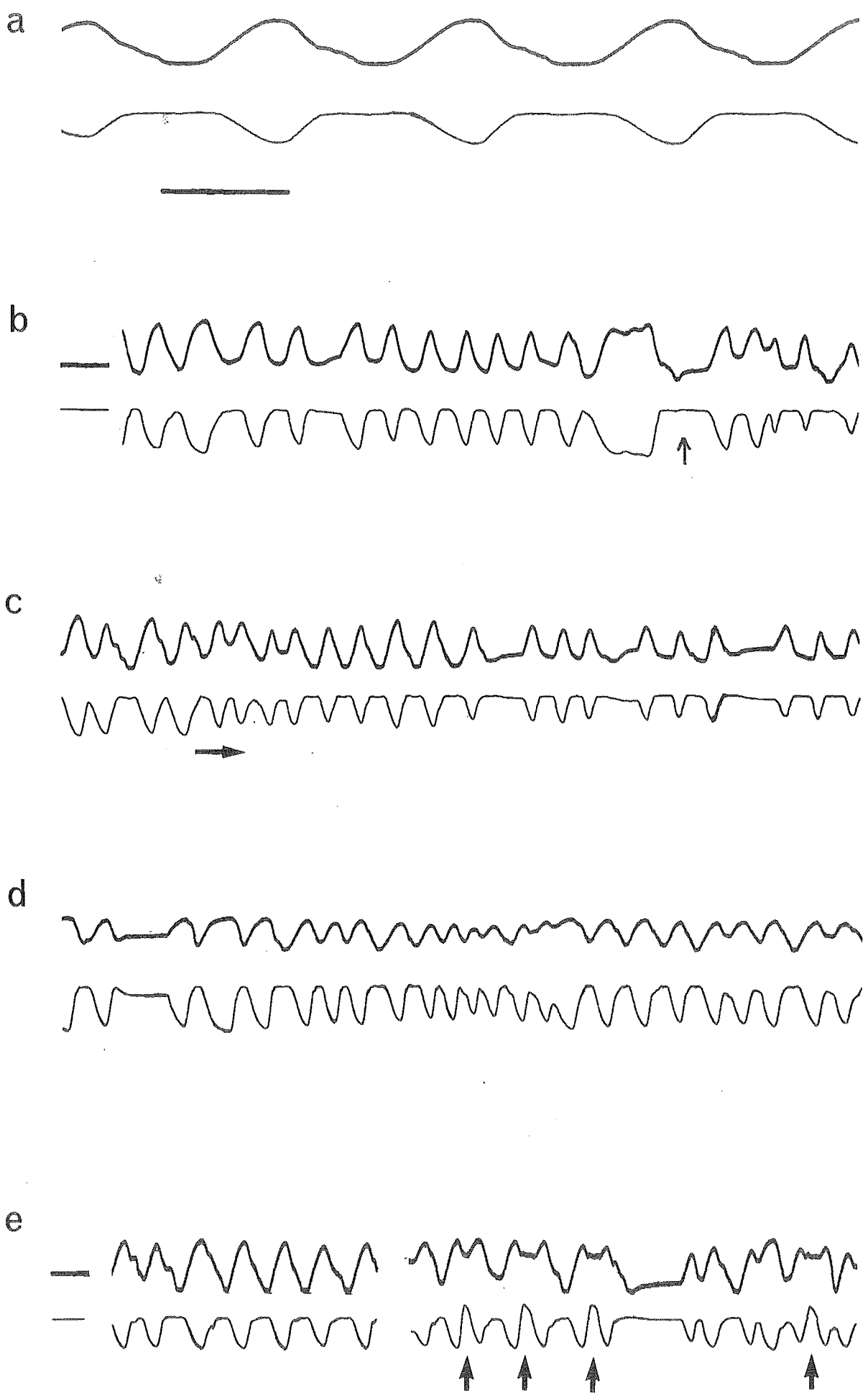
Calibration 5 seconds

(d) Chewing on apple following ablation of the right VMRO.

Calibration 5 seconds

(e) Chewing on apple following bilateral VMRO ablation. The arrows indicate bites where the left mandible has closed further than normally, preventing the right mandible from closing completely.

Calibration 5 seconds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mechanical properties from those found in the other substrates. The large diameter ensures a degree of mechanical coupling between the mandibles at a much wider gape than is usual in feeding. While the tube deformed readily it was never cut when bitten, thus preventing the usual degree of contact between the cusps. As one end of the tube was connected to a pressure transducer it could not be manipulated readily by the weta. Consequently bites were often irregular in form. The traces in Figure 40 (all from the same animal) show the sequences of tube biting most closely resembling mastication. A constant feature of all experiments involving rubber tube chewing was the pronounced phase lead of left mandible position in many of the more prolonged bites. As in mastication the left mandible reached a fully-closed position earlier than the right. Right closure then displaced the left. The size and resilient nature of the tube prevented the shearing action which would follow during feeding on apple. Complete right mandible closure here resulted in the enforced displacement of the left mandible to an apparently "open" position (see arrows Figure 40a). At this point the two mandibles were still mechanically coupled via the rubber tube. To the observer it appeared that the tube has been rolled between the mandibles from right to left. Simultaneous recordings from the pressure transducer attached to the rubber tube showed that sufficient force was exerted to collapse the tube until the walls met. Possibly the elasticity of the tube then contributes

to the opening movement of the left mandible. Whether or not this occurred the right mandible was clearly producing a stronger adduction force than the left.

No pronounced differences in bite form followed ablation of the right VMRO (Figure 40b). A similar asymmetry was observed, and the onset and completion of each bite were again approximately in phase. The right mandible showed a reduced excursion and the left closed more completely than before ablation.

In the bilaterally ablated animal (Figure 40c) the pronounced right to left displacement was replaced by a more symmetrical abuttal of the two mandibles, even during the longer bites. The pressure transducer readout (recorded on a different time scale) showed that the tube was still completely collapsed, but this alone does not imply that the same forces were developed as in the earlier traces. The absence of the asymmetrical bites could then be because lower forces were involved. Failing this, the altered pattern might result from disrupted positional information, perhaps due to the failure of the left VMRO to detect the influence of mandibular contact. This explanation would require that the output of the left VMRO partially inhibits the output to the left adductor muscles.

Not all the bites in the unablated condition showed the rolling effect. Several shorter duration bites, marked with a dot in Figure 40a, are approximately bilaterally symmetrical. Those illustrated produced full tube compression. Many similar short duration bites recorded in other traces did not. Up to 8-10 such brief,

weak bites may occur before a full closure bite. Inserting the tube between the mouthparts may also lead to behaviour resembling struggle chewing with purely unilateral bites occurring in either mandible. This may reflect the size and difficulty of manipulating the tubing.

Can the patterns of activity displayed in biting on a rubber tube be reconciled with that found in mastication? The essential difference between the two is in the nature of the displacement of the left mandible by the right on the more prolonged bites. In both regular mastication and the shearing-off manoeuvre the left mandible reached its most closed position earlier than the right, was then displaced slightly by right closure, but then regained full closure as the right begins to open (Figure 39a). Full left closure is thus continued during the early stage of right opening. Little force is here necessary to maintain the position of the left mandible. It follows then that a large elastic structure held in the mandibles would tend to displace whichever mandible is generating less force. Depending on the precise timing of force development in the two mandibles the same motor output would produce different patterns of movement in response to different chewing substrates. Thus the rolling bite of the rubber tube may not be as different from normal mastication as position-monitoring suggests.

IV APPLICATION OF ADDITIONAL LOADS

The regulatory capabilities of the mandibles were

Figure 40

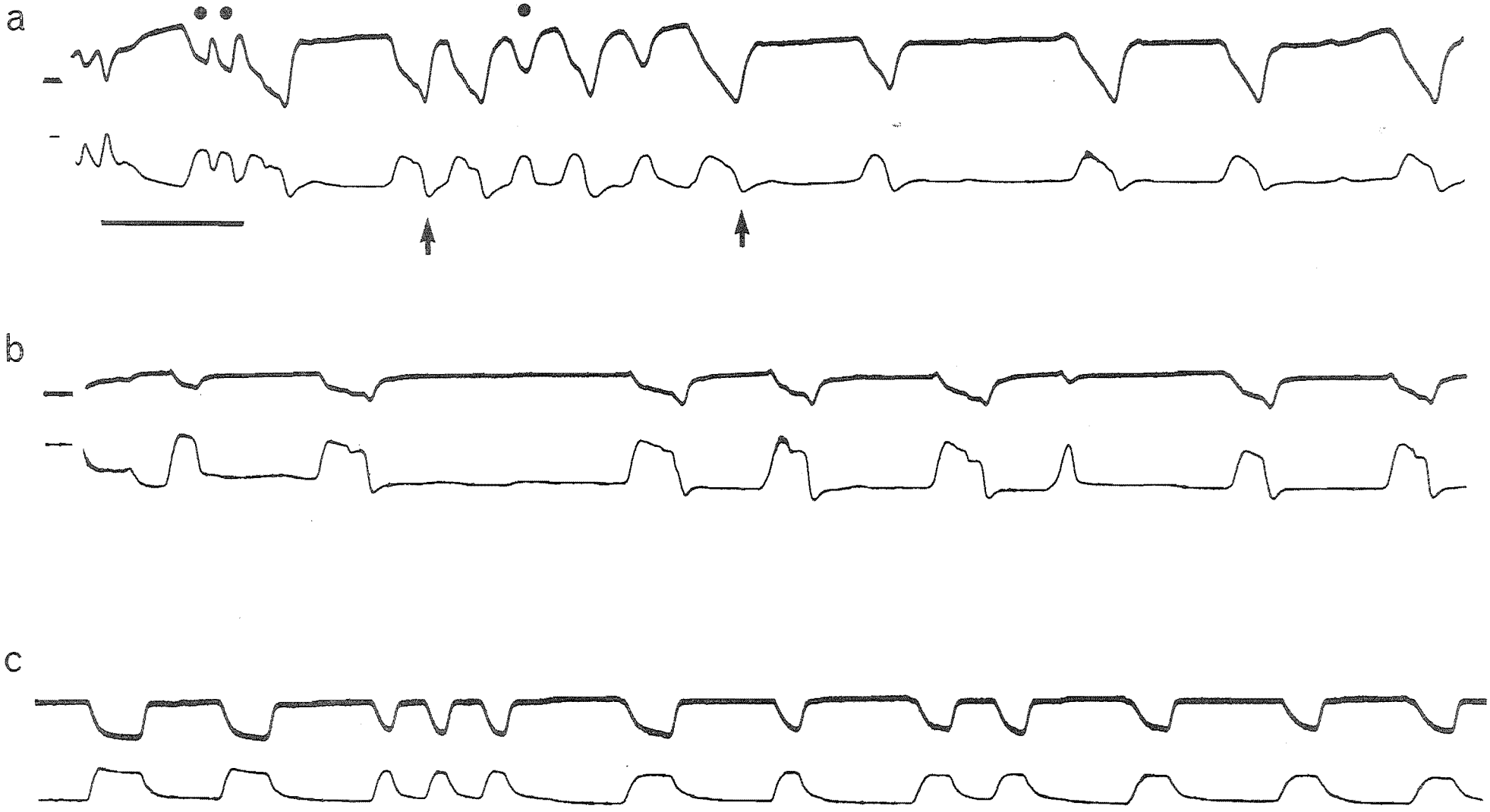
Chewing on a partially-compressible rubber tube before and after VMRO ablation.

The traces show mandible position. The right mandible is upper of each pair. Closure is toward the midline. Calibration 5 seconds.

(a) Before any ablation. The initial levels indicate mandibular rest position. Instances of extreme displacement of the left mandible by the right are indicated by arrows. The dots indicate full tube compression by symmetrical bites.

(b) Following ablation of the right VMRO.

(c) Following bilateral VMRO ablation.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examined in a series of loading experiments. Constant forces acting in the plane of opening were exerted by freely-hanging weights. These were suspended from fine threads passing over pulleys and attaching to the side of each mandible near the tip. Turning moments about the mandible hinge from approximately 5gm.cm to 55gm.cm could then be applied in the abduction or opening sense. These loads were trivial in comparison to the maximum recorded closing torques of more than 1000gm.cm. By monitoring mandible position under these conditions the load-compensating capabilities of the mandibular control system were tested.

Nine animals were tested. The weights were applied during quiescent periods with the mandibles in the "rest" position, and also during food-masticating sequences.

(1) Loading applied during inactivity

In all animals loadings of 55gm.cm caused wide opening with very small closure movements. Complete closures occurred during the struggling behaviour which often followed. Such closures were never sustained, and resembled chewing bites in their duration.

During rest the invariable response to even a 5gm.cm loading was an enforced opening of the mandible (Figure 41). This was followed by closure movements of varying velocity, frequency and amplitude. The velocity of both closure and the subsequent opening was much slower than during mastication. The amplitude of closure often varied from bite to bite and was never sustained. That is, a fully closed posture was never

Figure 41

Mandible movements in response to loading.

Freely-hanging weights attached to the mandibles by threads applied constant forces in the opening sense. Application of the force is indicated by an arrow directed in the opening sense (away from the midline). Unloading is shown by an arrow in the direction of closure (toward the midline). The right mandible is the upper trace in each case.

(a) Loading of the right mandible with firstly 10.4gm.cm and secondly 16.3gm.cm. The periods of bilateral activity in the second loading correspond to struggling behaviour.

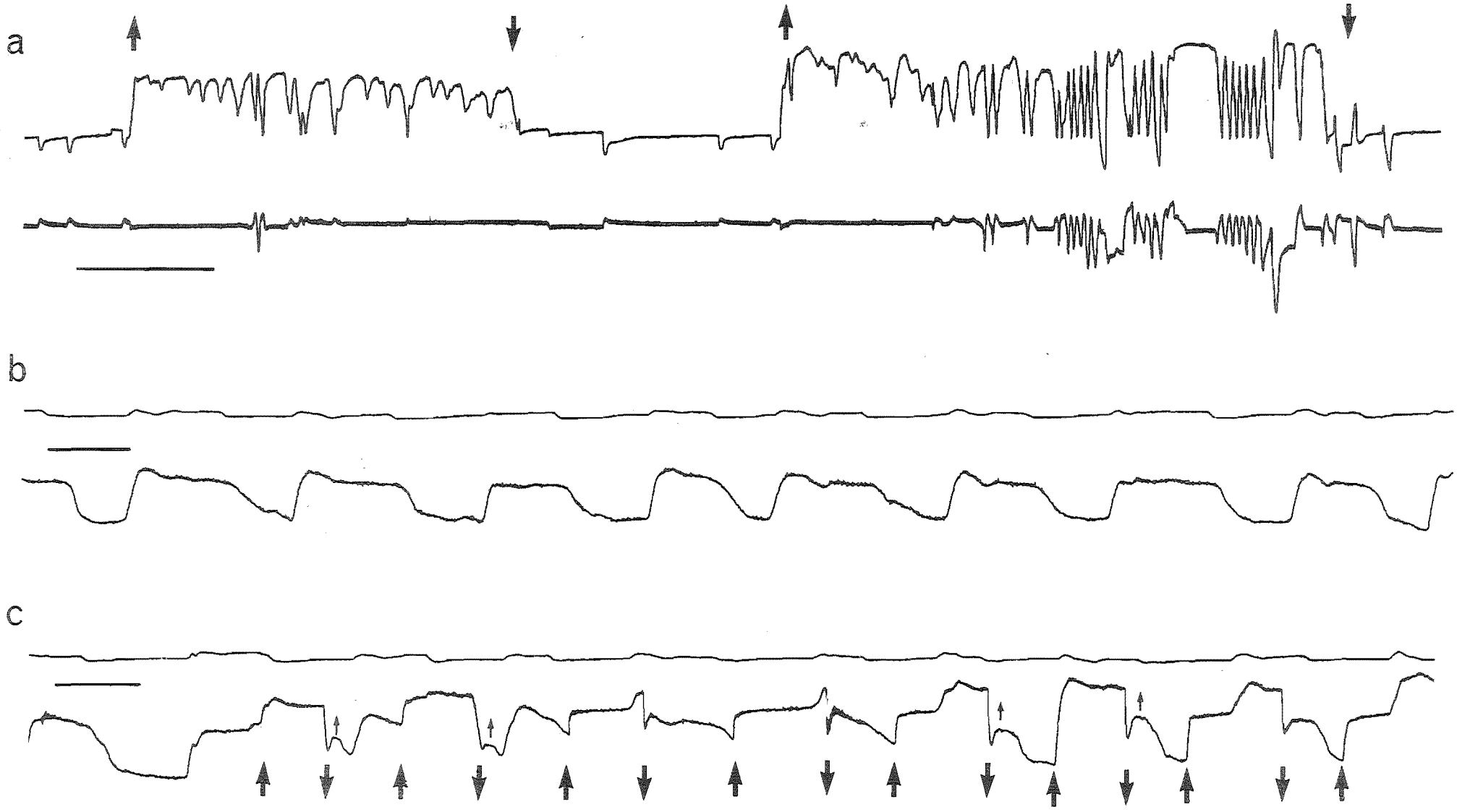
Calibration 25 seconds

(b) Spontaneous oscillations of the left mandible under a 13.1gm.cm load in a different preparation. The horizontal bar indicates the "at rest" position of the left mandible.

Calibration 5 seconds

(c) A continuation of trace 'b' but with the load repeatedly applied (arrow in the direction of opening) and removed (arrow toward the midline).

Calibration 5 seconds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maintained under load; slow irregular cycles of opening and closure were the usual pattern. No strict pattern of activity emerged. The mandible could remain passively in an "open" position for seconds before producing one to several closure cycles, to be followed by a further period of passive opening (Figure 41). At other times particularly at higher loadings the cycles were more frequent and/or more regular (Figure 41a,b). While the second trace illustrates a more regular cycle of activity the frequency (0.16Hz) is approximately one-sixth that of chewing, and in no case does any closure movement reach the 'rest' position for the left mandible. Unilateral loading usually produced a unilateral response, whether the left or the right mandible was loaded. The small deflections in the right mandible trace in Figure 41b are passive displacements from left mandible closure. However, unilateral loading while in a passive phase could elicit synchronised bilateral mandibular movements particularly when leg and antennal activity indicated greater arousal (Figure 41a). In experiments where the loads were repeatedly applied and then released, the unloading manoeuvre resulted in rapid and almost complete closure (Figure 41c) suggesting a weak tonic adductor muscle output. This might also account for the weak initial closure movements following load application (Figure 41c).

These experiments suggest that although the enforced displacement, can be detected, there is no accurate load compensating postural control system maintaining static position. The mandibles were never maintained in the 'rest' position or any other constant position

Figure 42

The effects of adding loads during mastication.

(a) Adding a 5.9gm.cm load to the right mandible. An arrow in the direction of opening indicates application of the load. Unloading is indicated by an arrow in the direction of closure.

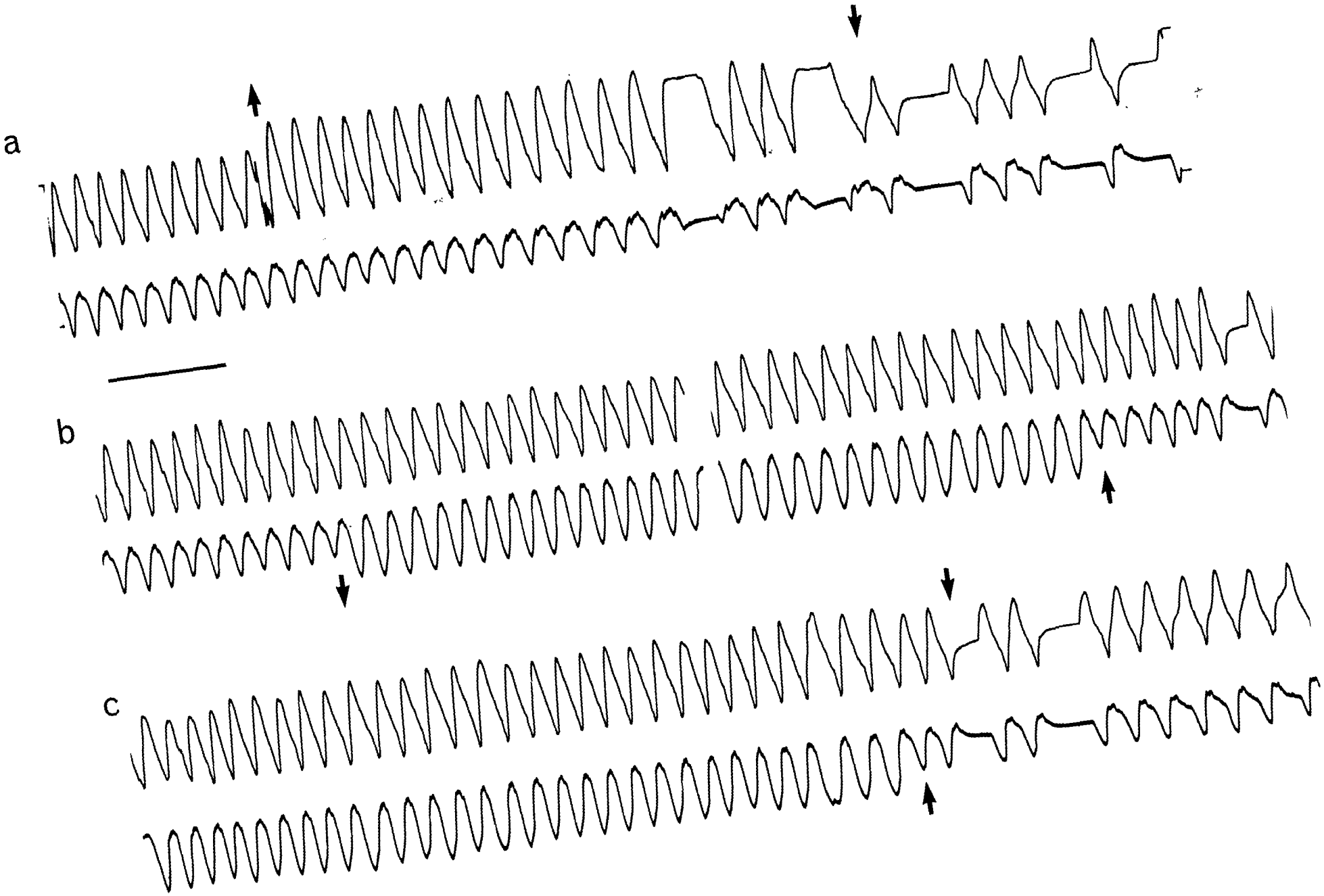
Calibration 5 seconds

(b) Loading of the left mandible with 15.1gm.cm. Arrows indicate the application and removal of the load.

Calibration 5 seconds

(c) Mastication with both mandibles loaded by 15.1gm.cm. Removal of the loads is indicated by arrows.

Calibration 5 seconds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while loaded and the variation in response to loading defies quantification.

One alternative explanation is possible. Myography suggests that the weakest mandibular movements are effected by the tentoro-mandibular muscle. While the tension it can develop has not been measured, its cross sectional area, line of action and location suggest that its peak contribution to the closure torque is approximately $4.0gm.cm^{-1}$. In making this calculation the value of $3kg.cm^{-2}$ for maximum muscle force was arbitrarily used, well above the figure of $2kg/cm^2$ derived for locust jumping muscle (Hoyle, 1973). Should the tentoro-mandibular muscle be responsible for maintained posture then the loads applied might still be beyond the sustainable output.

(2) Loads applied during feeding

The effects of loading during mastication are much clearer. Loads of 12-15gm.cm were routinely used. Adding this load during feeding on apple, lettuce or chicken produced two different patterns. In the first, chewing was disrupted for a few seconds before the cycle continued. Greater loadings increased the likelihood of complete inhibition of chewing. At other times the chewing cycle continued with little or no disturbance to the rhythm. Regular cyclical movements continued without pause particularly when the load was applied during opening. The load caused an immediate increase in the angle of opening on the loaded side only (Figure 42a,b). With unilateral loading the unloaded

side showed no distinct alteration in bite form.

The effects of unilaterally applied loads were largely confined to the loaded mandibles. The only possible evidence for a contralateral influence observed was a decrease in the amplitude of the unloaded bite excursion (Figure 42a). As the trace shows, the relationship between the amplitudes of the two sides is not consistent and the decreases are often small. In addition it is expected that bite amplitude will decrease during mastication as described above. Close scrutiny of the smaller amplitude bites shows that incomplete closure on the loaded side is matched by diminished closure on the unloaded side. It is in the extent of opening that the two sides differ. A small opening excursion on the unloaded side is often paired with a relatively large opening on the loaded side. The simplest explanation is that the load is maintaining a wide opening despite a reduced motor output to the abductor muscles of both sides. Whether this is induced by the loading or by a reduction in the size of the food bolus cannot be determined here. Attempts to measure relative amplitude before and after release of the load were thwarted by lack of a food which adequately resisted mastication. The long series of constant amplitude bites necessary for statistical analysis could not be obtained.

In the unloaded feeding experiments discussed above, increased amplitude of mandibular excursion resulted in lower frequencies. No consistent pattern of frequency change within or between animals was found with unilateral

left or right loading, or with bilateral loading, using loads of 12-15gm.cm which cause obvious amplitude changes. Data relating to the traces in Figure 42 are given in the following table.

Table 1

The Effects of Loading on Mastication

Loaded Mandible	Load (gm.cm)	Mean Frequency (Hz)	Sample Period (seconds)
left	0	0.97	25
	12.8	0.98	25
	0	0.98	5
right	0	0.96	8
	13.6	0.89	9
bilateral	0/0	1.11	6
(L/R)	12.8/13.6	0.96	15
	0/0	0.70	10

These data suggest that loading the right mandible can reduce chewing frequencies. Measurement of individual bite periods and analysis by the Mann-Whitney U test did not support this. Repeated runs gave varying results, including variations in the chewing rate in the unloaded condition. Increased rates of chewing under load were also recorded.

Any effect of this level of loading on chewing frequency is too small to distinguish from the

inconsistent baseline. Under loaded conditions, the opening excursion was increased without apparent decrease in the rate of mastication.

Greater loading than 12-15gm produced sequences of progressively decreasing bite frequency accompanied by pauses in which the loaded mandible was held open. This possibly indicates fatigue.

As the frequency is maintained during a greater excursion of opening then compensatory changes in bite form must occur. By fitting tangents to the slopes of the traces of mandible closure it was found that the principal change was an increase in the velocity of opening, achieved by sustaining higher velocities over a greater portion of the opening excursion.

V THREATENING AND DEFENSIVE BITING

Defensive biting often accompanies the mandible-gaping threat display, readily elicitable in wetas mounted on the head restraining apparatus. Visual and tactile stimuli each provoke both of these behaviours. The approach of the experimenter often causes gaping and rapid, incomplete biting movements.

Complete bites more commonly resulted from tactile input. A fine paintbrush stroking the frons or mouth-parts was routinely used to evoke this behaviour. Both these behaviours are shown before and after VMRO ablations in Figure 43. The defensive display involved prolonged, wide mandible gaping of approximately symmetrical form.

Figure 43

Threatening and defensive biting in an animal held in the restraining device.

(a) before ablation

(b) following right VMRO ablation

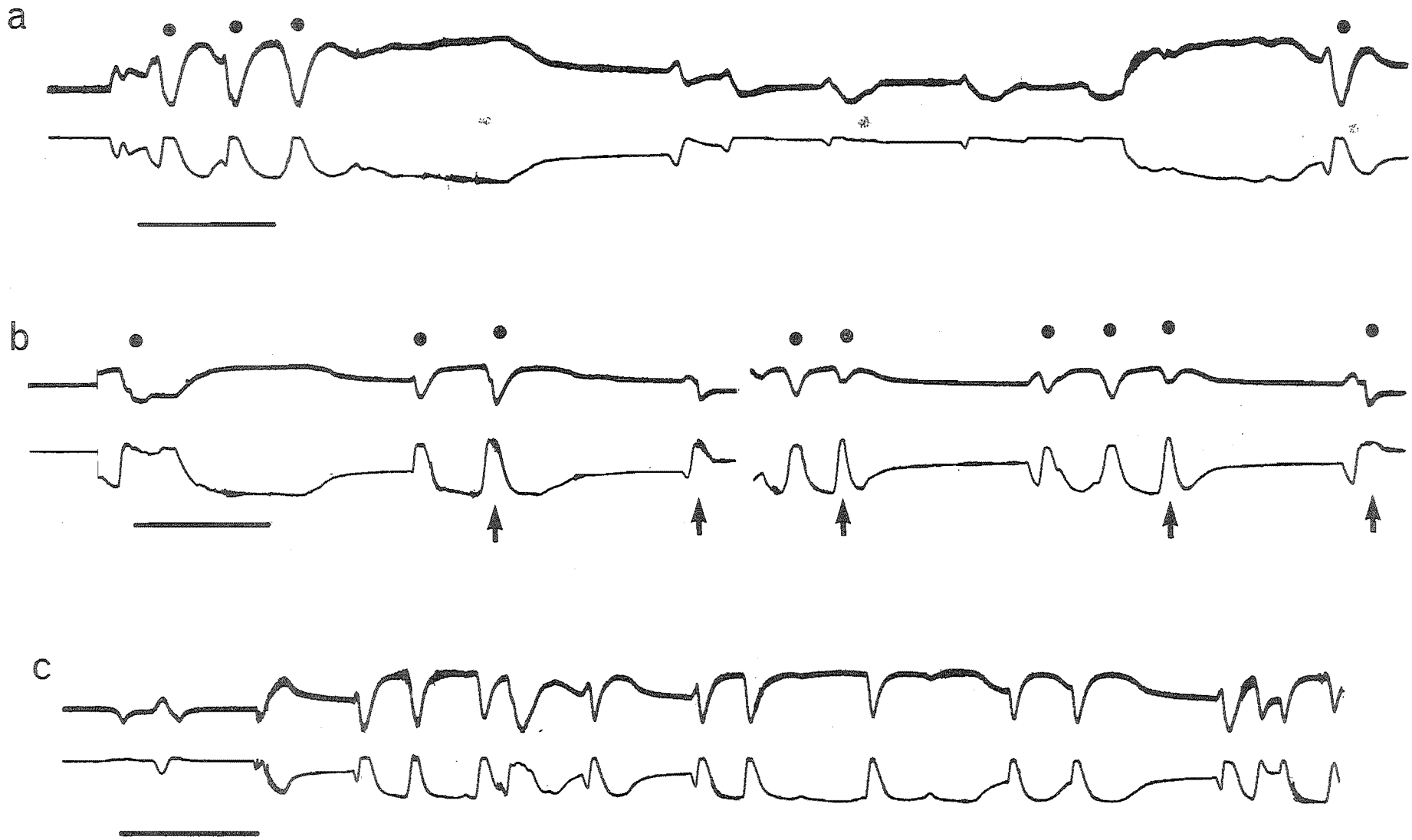
(c) following left (bilateral) VMRO ablation

The "rest" position for each mandible is given by the steady level beginning each trace.

The right mandible is the upper trace of each pair. Closure is toward the midline. Defensive bites are indicated by dots.

The arrows indicate mismatching of the mandibles, where the left closes inside the right.

Calibration 5 seconds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The maximum angle of opening in the threat display was measured before and after VMRO ablation in 15 animals. No consistent pattern of alteration emerged and the pooled data showed no significant change following ablation.

The possible involvement of the VMRO in this behaviour cannot be excluded. Evidence from three preparations, including that shown in Figure 43b suggested that the extent of gaping may be influenced by unilateral VMRO ablation, as here right mandible opening was reduced. However the angles of opening are not necessarily symmetrical (see Chapter III) and central motivation determines the extent of opening. Wide gaping is still possible after bilateral ablation (Figure 43c). While VMRO ablation may influence opening angles in a subtle manner it was not possible to distinguish any such proprioceptive effect from habituation due to experimental handling.

The defensive bite involves rapid, complete closure from a widely gaped position. The lack of a food bolus or similar object precludes the possibility of mechanical coupling of the mandibles through an intermediate structure. The bite then requires precise coordination of the fully-closed position at the end of a higher velocity movement of wide excursion, perhaps the most extreme test of positional coordination the unloaded system faces.

The defensive bite occurs in two forms, the first of which is illustrated in Figure 43a. A rapid closure

was followed closely by rapid opening, with cusp contact sustained for no more than 0.4 secs. Although these were the fastest closure rates observed, the period of unopposed adduction varied from 0.2-0.5 seconds. Peak angular velocities reached $150^{o}.sec^{-1}$, but values around $40^{o}.sec^{-1}$ were more common. These rates are little different from the fastest velocities observed during feeding.

The second form of defensive bite is well illustrated in the first bite in Figure 43b. A sustained closure is maintained for 2 seconds, to be followed by a threat. A sequence of up to 4-5 such prolonged bites may follow without release of the object during the relaxation phase.

The effect of right VMRO ablation on defensive biting is shown in Figure 43b. Those closures marked with an arrow indicate bites where the mandibles did not intermesh in the normal manner. The position of contact was with the left mandible closed past its normal position, preventing the right from closing completely. In this situation the tips of the mandibles interlock, preventing the normal shearing action. This was occasionally observed in struggling behaviour in the intact animal. Following left VMRO ablation this mismatching phenomenon was lost (Figure 43c). In numerous defensive bites an apparently normal pattern was maintained.

Not all VMRO ablations produced the pattern presented here. While mismatching commonly results from ablation, it is not unique to unilateral right

ablation. It may appear only after bilateral ablation. The extent of shortening of the ablated VMRO may be more influential in determining the pattern than which receptor is ablated.

VI DEFENSIVE BITING WITH THE MANDIBLES RESTRAINED

The format for the presentation of results in this section has been determined by the nature of the responses. In general, particular effects are described with respect to individual preparations and variations from this pattern noted. In explanation of this it is necessary to anticipate some of the results described in ensuing sections.

While induced defensive biting in intact animals showed a rigid and repeatable pattern, both within and between individuals, the responses to VMRO ablation were more varied. The ablations appeared to alter the perception of mandibular position to the extent that bilateral responses did not always occur in the position from which the preablation base data were collected. To achieve bilateral biting it was necessary to alter mandibular position. However, alteration of mandibular position also affected the biting in ablated animals. Data collected following an alteration in the position of the mandibles have been subjected to changes in two variables, the ablation and the change in position.

The effects of VMRO ablation are described with respect to two preparations illustrating general trends. Both of these preparations were successfully ablated in both mandibles. Both then produced bilateral bites

in the positions from which the base data were collected. In contrast, a more extreme result was found in one preparation where bilateral biting did not occur consistently in any combination of mandible positions (Figure 49). The effect of unilateral right ablation was different from that of the left. The preparation to show the effects of ablating the right VMRO first is a conservative example compared to that in Figure 49. The preparation illustrating the generally less disruptive left ablation was chosen because it showed the most pronounced effect of this ablation, while still producing bilateral biting.

(1) Duration of induced defensive biting

(a) Bilateral biting in the intact animal. Defensive biting can be readily provoked where the weta is held in a head cast and the mandibles are prevented from closing by a rigid obstruction. This aspect of behaviour can be exploited to record bite force. Each mandible is coupled to a transducer by an inextensible rod (See Chapter II) thus allowing independent but simultaneous measurement of the forces developed in the two mandibles. Under these conditions the weta is biting onto two rigid immovable metal wires approximately 0.7mm in diameter. By stroking the frons, or less commonly, the mouthparts with a fine paintbrush, defensive biting can be elicited repeatedly for several hours, provided brief rests are allowed. Provided the mandibles are held more than about 10^{o} open, the bites produced have a highly consistent pattern which is

maintained with little variation over hundreds of bites. All the twenty-two animals tested produced essentially the same pattern (Figures 44, 45). A pen recorded trace of a bite shows torque development has an approximately sigmoid form with the initial slower rise giving way to a rapid, approximately linear phase before the rate slows near the peak torque (Figure 45a). The time of onset of the bite is difficult to determine, particularly as there may be a low level of adductor muscle activity sustained between bites (see myography, Figure 21d). However the interval between bite onset and peak force was close to 0.2 seconds for the bites in Figure 45a. The interval from 10% force, which can be defined more precisely, to full force is 0.15 sec for all three right mandible bites. Forces developed were invariably high in all animals. These are expressed as moments (or torque) about the mandibular hinge to control for variations in the distance from the hinge to the contact point between the mandible and the force transducer coupling. All three left mandible bites in Figure 7a developed 1105gm.cm, the figure being 1029gm.cm for each right bite. Such consistency is unusual. A series of eight bites from the same animal taken immediately before this gave values of 1180 ± 32gm.cm (left mandible) and 1006 ± 43gm.cm (right mandible). Concealed in this figure was a steady decline in strength of bite from a maximum of 1255gm.cm for the first left mandible bite to the minimum of 1130gm.cm for the last. Declines in torque within a single sequence were commonly found and were probably due to fatigue. For this reason bite sequences were usually

limited to 8-10 bites. The original levels could be restored after a rest of approximately a minute. Not all sequences showed this decline. Failure to bite either through habituation or fatigue never prevented a preparation being used, although bite strength often declined after prolonged testing, including ablations.

The initial biting moments quoted above are typical of what was recorded in all animals and much less than the maximum of 1900gm.cm. Measured torque varied with the angle of opening and with the relative position of the two mandibles (discussed below). In all experiments in this section the mandibles were held partly open by approximately similar amounts to ensure that bilateral biting always occurred. In this situation defensive bites of less than 800gm.cm were uncommon in rested, unoperated animals.

Unlike the situation where the weta could close its mandibles fully onto a soft object, defensive biting onto a transducer did not normally result in sustained torque development. Relaxation followed immediately after the maximum torque was reached. Relaxation took approximately twice as long as the active phase of biting, measuring to the 10% of maximum torque level. The maximum rate of relaxation was also close to half that of torque development, comparing the slopes of tangents fitted by eye to the pen-recorded traces. The final stages of relaxation were the most variable both within a single preparation, and between different animals. Precisely defining the end point of a bite was difficult, if not impossible

Figure 44

Induced defensive biting with the mandibles restrained by rigid force transducer couplings.

The right VMRO is ablated first.

The mandibles are held open from the rest position by 17^{o} (right) and 10^{o} (left). The right mandible is the upper trace in all bilateral biting sequences. Horizontal calibration: 1 second in all traces. Vertical calibration: 1000gm.cm in all traces.

(a) Bilateral biting in the unablated condition.

(b) Unilateral biting by the right mandible.

(c) Unilateral biting by the left mandible.

(d) Bilateral biting following ablation of the right VMRO.

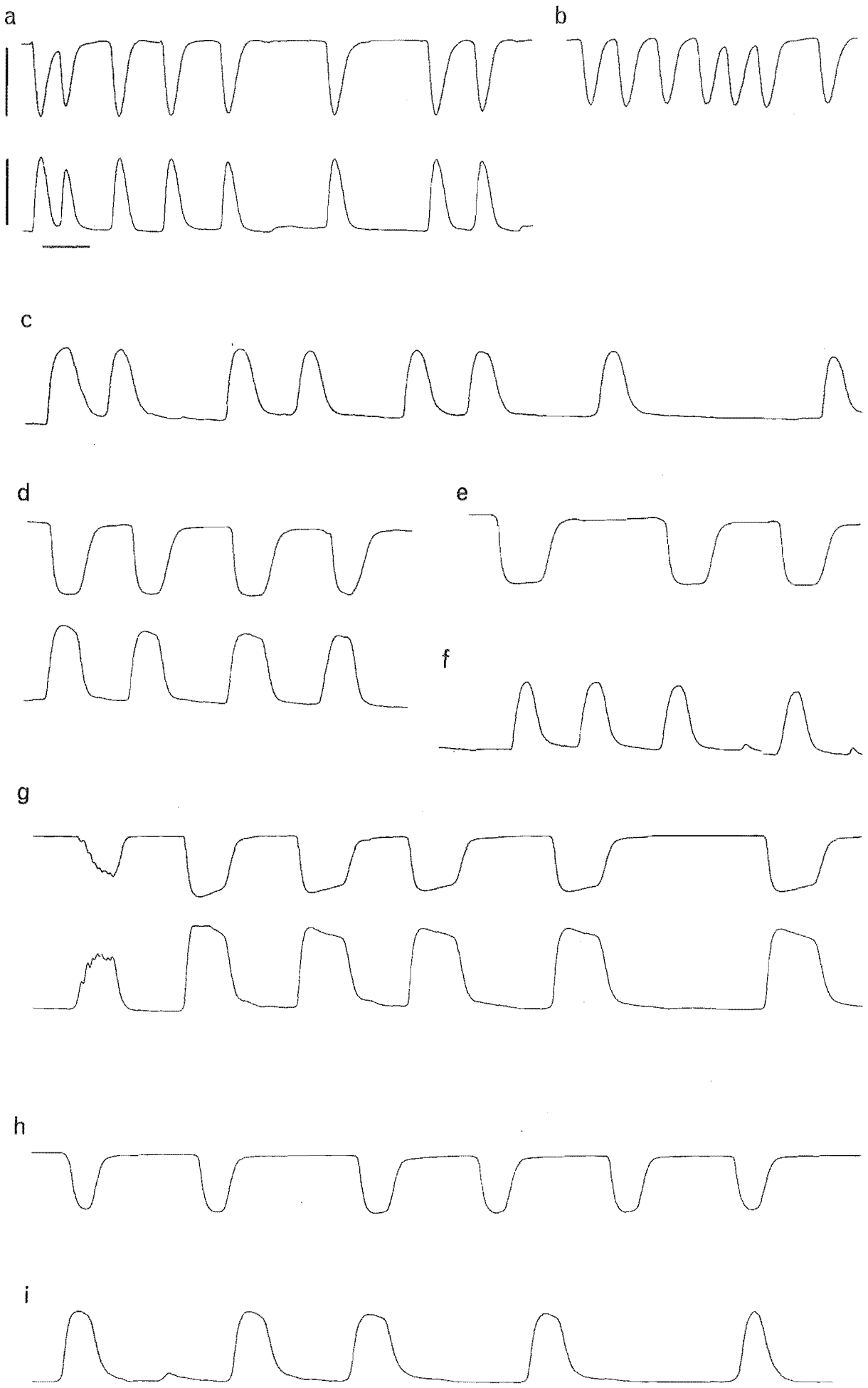
(e) Unilateral biting by the right mandible following ablation of the right VMRO.

(f) Unilateral biting by the left mandible following ablation of the right VMRO.

(g) Bilateral biting following ablation of both left and right VMRO. The first bite in the sequence is a spontaneous closure.

(h) Unilateral biting by the right mandible following ablation of both left and right VMRO.

(i) Unilateral biting by the left mandible following ablation of both left and right VMRO.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as the pre-bite resting level was often not resumed in most preparations. This may be due to a sustained low level of muscle activity (see myogram Figure 21c). For this reason the measure of bite duration used is the interval from when half the maximum torque has been developed to when the same value is reached during relaxation (see Figure 45a). This statistic, D, is relatively insensitive to variability in the first and last stages of the bite, and also in the shape of the peak of the recorded waveform. It is affected by changes in amplitude. Where these were marked within a sequence the ratio D/maximum torque was sometimes used to obtain a measure of bite form that was most sensitive to the prolonged maintenance of high levels of torque. It is also sensitive to alterations in the rates of torque development and relaxation. Biting sequences partially represented in Figure 45b gave values of 0.25 ± 0.02 sec (right mandible) and 0.30 ± .01 sec (left mandible) while the sequence shown in Figure 44a gave 0.29 ± 0.03 sec (right) and 0.30 ± .02 sec (left) (n = 8 in both cases). The highest mean value recorded for D in any preparation with well opened mandibles was 0.42 sec. These data confirm what is shown in the pen-recorder traces; the form of the defensive bite was very consistent under the stated conditios. A further characteristic of all defensive biting was that torque was developed very evenly. It was unusual to record ripple or 'staircase' effects. Occasionally these appeared near the peak of torque development but never in the rapidly rising

phase. Irregularities of this sort often appeared in spontaneous bites of lower amplitude and slower rates of tension development (e.g. Figure 44g). This suggests that the defensive bite may depend on a different motor programme and is perhaps a ballistic manoeuvre which is not influenced by peripheral feedback at least during its early stages.

Exceptions to the typical pattern of the defensive bite were recorded infrequently. If the mandibles were held so that they almost met in the midline the peak torque was sometimes maintained in an irregular plateau for a period still less than a second. The rates of torque development and relaxation were not altered. Using a surgical silk transducer coupling looped over the mandible also prolonged the bite, particularly in positions of almost complete closure. This coupling stretches slightly under load, allowing a small amount of closure, quite different from the inextensible metal rod normally used. Longer bites occurred early in an experiment if they occurred at all, and usually in the first bite of any sequence, suggesting that the weta may learn to recognise some property of the transducer apparatus.

It is usual for the partially-opened mandibles to rest against the transducer coupling. However, if the animal is sufficiently excited the mandibles may be gaped more widely in the threat display. In a defensive bite from such a position the mandibles may be moving rapidly when they first contact the transducer coupling. In this case there was a precisely-defined onset of each bite on the chart recorder trace. This

Figure 45

Induced defensive biting with the mandibles restrained by rigid force transducer couplings.

The left VMRO is ablated first.

The mandibles are held open from the rest position by 14^{o} (right) and 17^{o} (left). The right mandible is the upper trace in all bilateral biting sequences. Time calibration in traces b-j, 1 second.

(a) Bilateral biting in the unablated condition. Time calibration 0.2 seconds.

(b) Bilateral biting in the unablated condition. Calibration 1.0 seconds.

(c) Unilateral biting by the right mandible.

(d) Unilateral biting by the left mandible.

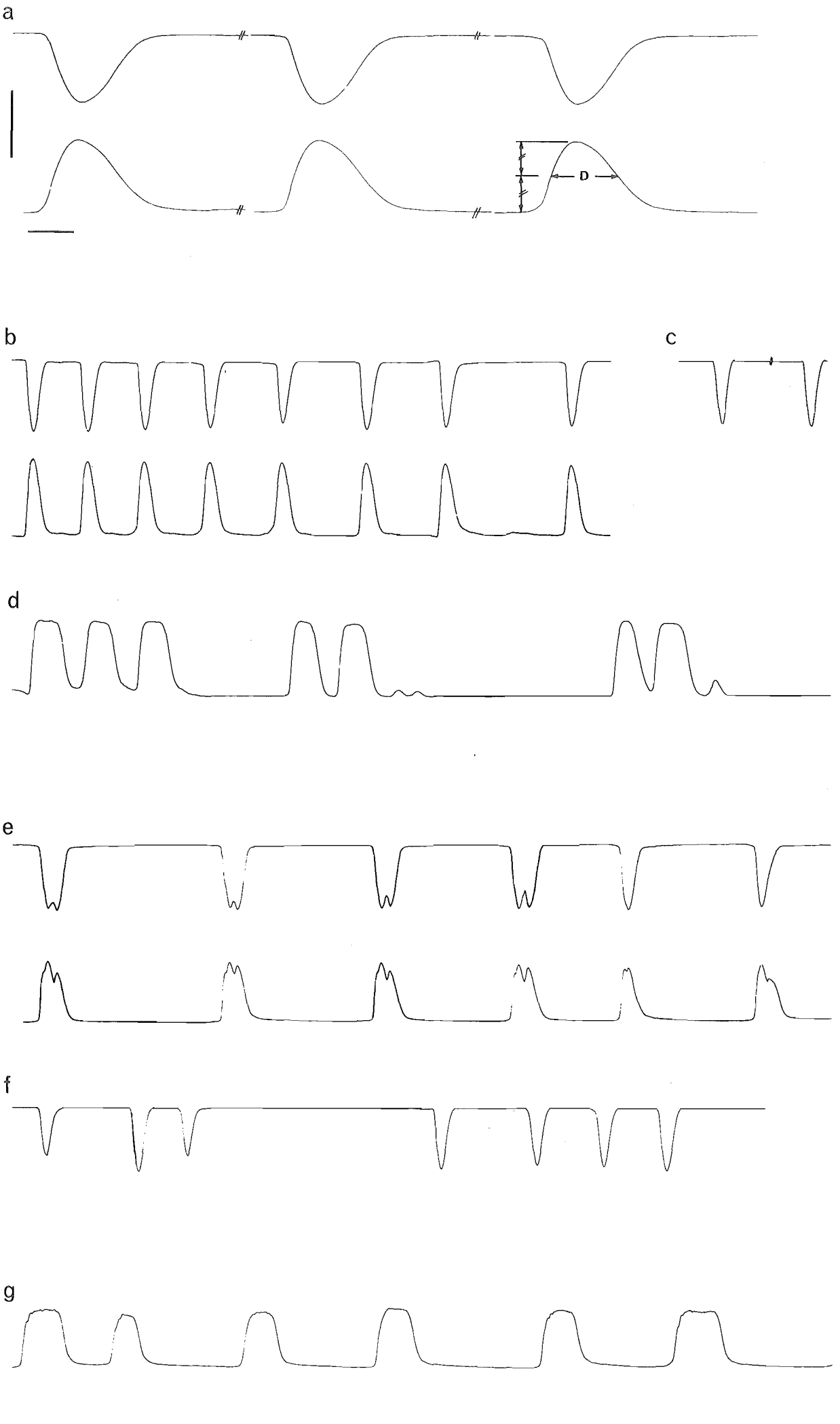
(e) Bilateral biting following ablation of the left VMRO.

(f) Unilateral biting by the right mandible following ablation of the left VMRO.

(g) Unilateral biting by the left mandible following ablation of the left VMRO.

Continued . . .

The measurement of the statistic D is shown in trace (a).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. . . Figure 45 continued

(h) Bilateral biting following ablation of both left and right VMRO.

(i) Unilateral biting by the right mandible following ablation of both left and right VMRO. The additional two bites show the preablation response.

(j) Unilateral left biting by the left mandible following ablation of both left and right VMRO.

Horizontal calibration (all traces): 1 second.

Vertical calibration (all traces): 1000gm.cm.

Figure 46

The effect of mandibular position and VMRO ablation on the phasing of torque development in induced defensive biting. All records are from the same preparation.

(a) Unablated condition, mandibular positions right = 14^{o}, left = 17^{o} open from rest.

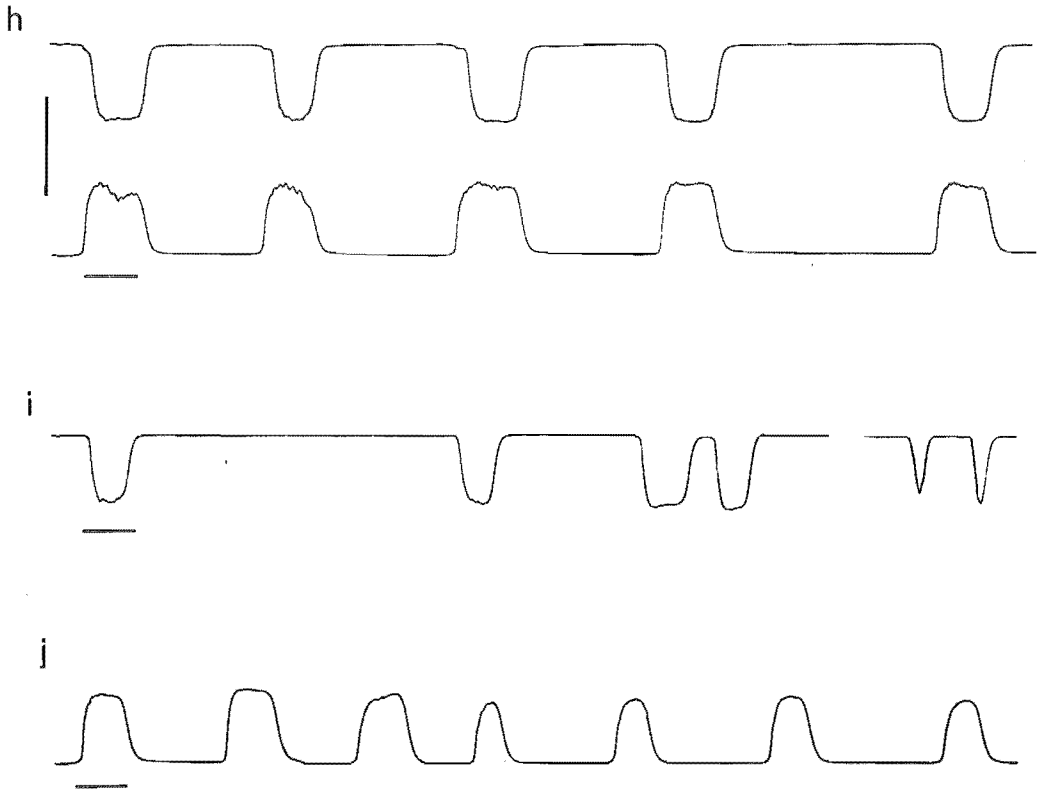
(b) Following left VMRO ablation positions as in 'a'.

(c) Following left and right VMRO ablations, positions as in 'a'.

(d) Following left and right VMRO ablations, positions altered to right = 20^{o}, left = 17^{o} open from rest.

(e) Following left and right VMRO ablations, positions altered to right = 29^{o}, left = 2^{o} open from rest.

The vertical dashed lines are arbitrary time reference points. The time scale is one second.



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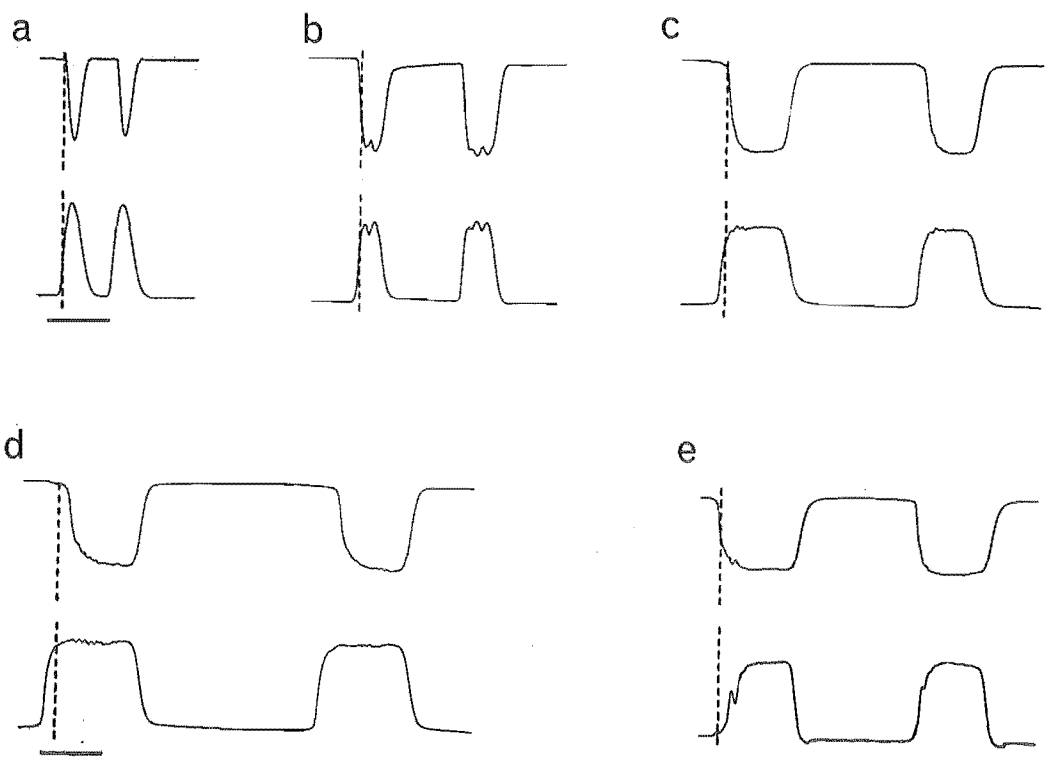


was the only apparent effect on the recorded bite. No greater maximum rates of torque development were found, and bite durations were not significantly shorter.

Following VMRO ablation, wide gaping led to bites where the mandibles closed rapidly until they contacted the transducer coupling, but failed to develop measurable tension after contact was made.

(b) Unilateral biting in the intact animal. Defensive biting could be elicited when only one mandible was in contact with a force transducer and the other was completely unrestrained. This is termed unilateral biting. Each mandible produced a unilateral bite of characteristic form, the left differing from the right. Right unilateral bites were identical or closely similar to bilateral bites (Figures 44b, 45c). Any variation was usually a slightly longer duration but the increase was never great (see, for example Table 2).

The left unilateral bite was typically approximately twice the duration (measured at half peak torque) of the bilateral bite (Table 2). Maximum rates of torque development were similar but in the unilateral situation the higher rates were sustained for shorter periods. This was particularly evident towards the peak torque development where the pen recorder trace appeared more rounded than in bilateral biting (Figure 44c). Left unilateral bites were always longer than right unilateral bites. Increases as little as 30% longer than in bilateral biting were recorded from left mandible unilateral bites.

Table 2

The duration of induced defensive biting before and after VMRO ablation. The right ablation was performed first. The mean duration of the bites within each sequence is given in seconds, and is measured at half peak torque. The mandible positions are: right 17° open from rest; left 10° open from rest.

		$\bar{x}$	σ_{n-1}	n
Before ablation				
bilateral	r	0.29	±0.03	8
bilateral	l	0.30	±0.02	8
unilateral	r	0.33	±0.01	8
unilateral	l	0.56	±0.05	8
Right VMRO ablated				
bilateral	r	0.83	±0.05	8
bilateral	l	0.87	±0.04	8
unilateral	r	1.01		3
unilateral	l	0.56	±0.03	8
Left VMRO ablated				
bilateral	r	1.09	±0.05	
bilateral	l	1.10	±0.05	7
unilateral	r	0.62	±0.05	6
unilateral	l	0.77	±0.06	5

(2) The effects of ablation on bite duration

Ablation of the right VMRO increased the duration of both right unilateral biting and bilateral biting. The animal shown in Figure 44d showed an increase in D of almost three times the preablation value for bilateral biting (Table 2). The durations of the left and right bites were not significantly different during bilateral

biting, although close inspection of Figure 44d shows that the phasing at onset and peak torque was not always exact. Phasing is discussed in more detail below. Unilateral bite durations were now markedly different on the two sides. The left mandible alone showed no difference from the preablation value, and it is now significantly shorter than the duration of the bilateral bite ($p < 0.01$). In contrast the right unilateral bite was of a greater duration than even the bilateral bite, which therefore lies between the values recorded for the two sets of unilateral bites.

Subsequent ablation of the left VMRO increased the duration of both the left unilateral bite and the bilateral bite. In the latter case the increase was small in comparison to the effect of the initial operation. Although the right mandible was not further operated on, the duration of the unilateral right bite was much shorter than before ablation of the left VMRO (0.62 vs 1.01 seconds, $U = 0$ $p < 0.01$). The duration of the bilateral bite was no longer intermediate between the values found for the left and right sides independently, nor was it at all close to either of them.

The effects of similar VMRO ablations carried out in reverse order, left preceding right, are shown in Figure 45 and Table 3. These data relate to one animal selected because it showed the most extreme influence of unilateral left VMRO ablation on the bilateral bite.

In this preparation the values of D recorded from the intact animal during bilateral biting were not exactly

the same, the left being fractionally greater (right, 0.25; left, 0.30). When corrected for amplitude the values became 0.25 sec (right) and 0.26 sec (left). The unilateral right bite was again essentially the same duration as the bilateral bite, while the left duration approximately doubled.

Table 3

The effect of VMRO ablation on the duration of induced defensive biting. The left ablation was performed first. The mean duration ($\bar{x}$) and standard deviation (σ) of the bites within each sequence is given in seconds and measured at half peak torque. The mandible positions are: right, 14° open from rest; left, 17° open from rest.

		$\bar{x}$	σ_{n-1}	n
Before ablation				
bilateral	r	0.25	±0.02	8
bilateral	l	0.30	±0.01	
unilateral	r	0.23		2
unilateral	l	0.65	±0.07	7
Left VMRO ablated				
bilateral	r	0.44	±0.05	10
bilateral	l	0.43	±0.06	
unilateral	r	0.25	±0.01	6
unilateral	l	0.91	±0.11	6
Right VMRO ablated				
bilateral	r	0.90	±0.09	7
bilateral	l	1.07	±0.11	
unilateral	r	0.71	±0.11	4
unilateral	l	0.76	±0.16	9

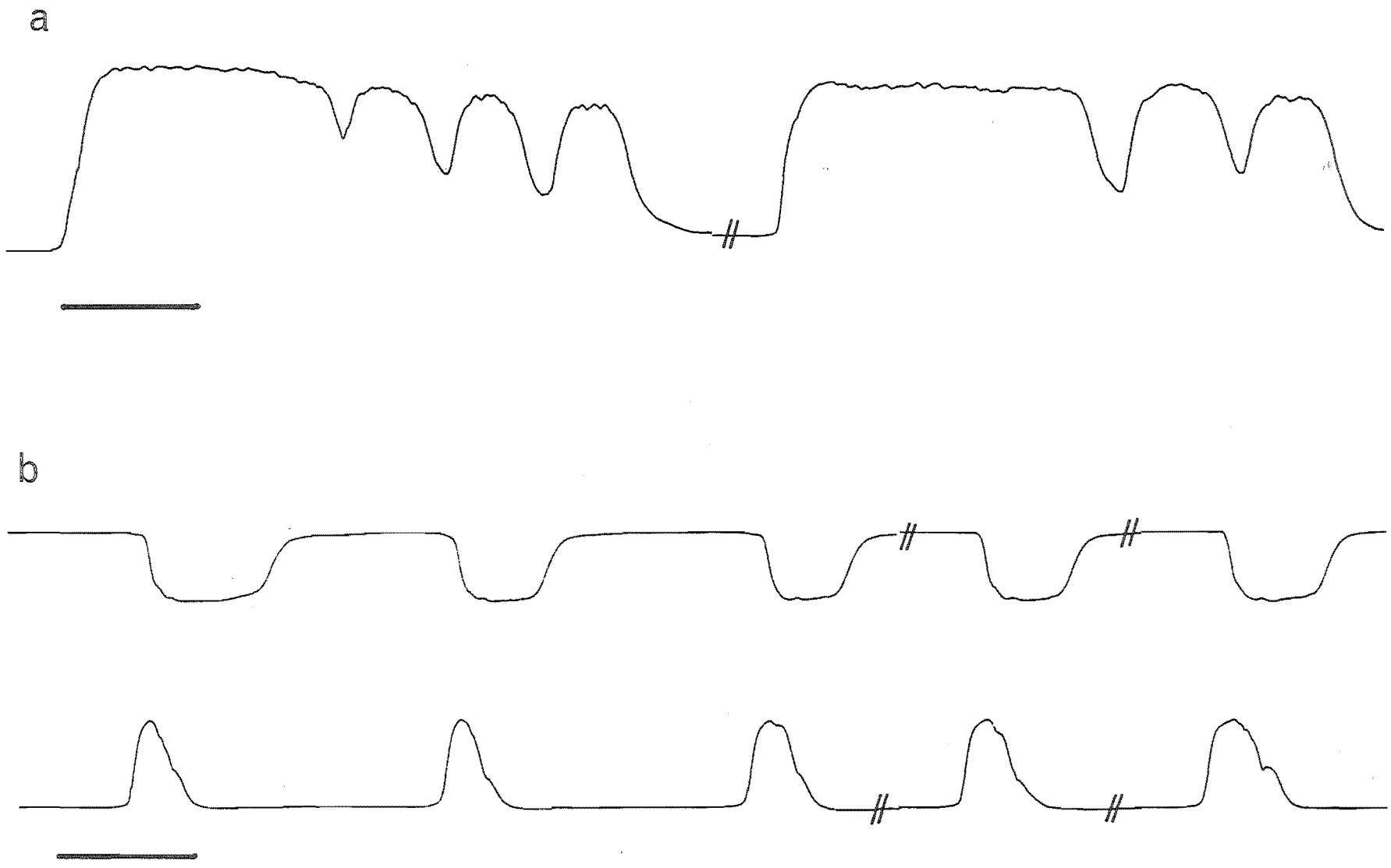
Figure 47

(a) Unilateral biting by the left mandible following left VMRO ablation. These are the longest recorded bites of any sort. The two long bites were accompanied by complete right mandible closure (not illustrated). Left mandible position, 24^{o} open from rest.

Calibration, 1 second

(b) Bilateral biting following ablation of the right VMRO and both ventral groups of campaniform sensilla. Torque development and relaxation are both out of phase. The right mandible is the upper trace.

Calibration, 1 second


a
b

Ablation of the left VMRO had no effect on unilateral right biting but the left bite was prolonged by an average of 40% for the first 6 bites. The durations were not highly consistent. The bilateral bite duration is also longer, although it is only half that found in the example with a unilateral right VMRO ablation (Table 2). In spite of this, the example shown was the most extreme alteration obtained from a unilateral left VMRO ablation. Examination of the trace in Figure 45e shows a number of bites having more than one peak, particularly those earlier in the series. Further, the multiple peaking is more prevalent in the operated (left) than in the unoperated (right) side. The pattern of decreasing bilateral bite duration and the increasing tendency to produce single peaks during a sequence was unchanged 24 hours after the initial operation.

The effects of left VMRO ablation on bilateral biting in other animals were variable. Some sequences were essentially the same as before the ablation, even where unilateral left bites were markedly affected. The data in Table 4 illustrate this well. In the intact animal the bites were of short duration, even the unilateral left bite being only 30% longer than in the bilateral bite. Following left VMRO ablation the bilateral bites altered little, yet the unilateral left bites increased greatly. The mean duration of 1.28s) was obtained from the sequence shown in Figure 47a. This shows the longest unilateral bites recorded in any preparation. The lower value, 0.69s refers to another sequence recorded under the same conditions.

The extreme values were not repeated but the duration was still significantly longer ($U = 0$, $p < 0.01$) than before ablation and the variability is high.

Table 4

Duration of induced defensive bites within sequences taken before and after left VMRO ablation. The mean duration at half peak torque is given in seconds.

		$\bar{x}$(s)	σ_{n-1}	n
Before ablation				
bilateral	r	0.27	±0.01	6
bilateral	l	0.22	±0.01	
unilateral	l	0.29	±0.03	8
After ablation				
bilateral	r	0.25	±0.05	7
bilateral	l	0.28	±0.02	
unilateral	l*	1.28	±0.96	6
unilateral	l*	0.69	±0.22	7

* These two values were obtained from different sequences with the left mandibles in the same position.

Other results of left VMRO ablation included sequences of bilateral bites where a weak tendency to produce twin-peaked bites was apparent early in the sequence but not thereafter. In one preparation, consistent bilateral biting was not seen following left VMRO ablation.

The preparation listed in Table 3 had the left VMRO ablated first. Subsequent ablation of the right

VMRO produced a similar biting pattern to that listed in Table 2 (bilateral ablation, right ablated first). Bilateral biting was substantially prolonged, with D at least double the values recorded following the single ablation and approaching four times the initial duration. Following bilateral oblation the durations of the left and right bites were not equal during bilateral biting, the right being shorter in every case and the left and right groups being significantly different ($U = 5$, $p < 0.01$, data in Table 3).

Both the left and right unilateral bites were shorter than in bilateral biting (left $p < 0.01$; right, $0.01 < p < 0.05$). Although the mean duration of the left unilateral bite was much shorter than before the right VMRO ablation the differences are not statistically significant.

(3) Phasing of induced defensive biting

The phasing of the two sides in bilateral biting was always close in the unablated condition when the mandibles were symmetrically disposed. A left mandible phase lead of less than 0.02 seconds was found in all animals, whether measured at peak torque or at half peak torque. This latter measure was preferred to eliminate the difficulties in determining the precise onset of biting, and also the peak torque in the more prolonged bites resulting from ablation.

A series of bites from a single preparation is shown in Figure 46. The phasing varied from a left mandible lead of less than 0.02s ($n = 8$) to an increasing left

lead following bilateral ablation (left lead 0.14 ± 0.04 sec, n = 9). The appearance of a pronounced left phase-lead was a frequent but not invariable result of VMRO ablation. There was no appreciable phase alteration in the example in Figure 44. Mandibular position had a pronounced influence on any phase difference resulting from VMRO ablation. A further six degrees of opening to the right mandible (Figure 46d) increased the left phase lead from 0.14s to 0.26 ± 0.04s, while extreme opening of the right mandible coupled with closure of the left altered the phase relationship so that the right mandible led (Figure 46e). Occasionally manipulation of the mandibular position in this manner resulted in similar phase changes in unablated animals. However the typical response was maintenance of close phasing until a position was reached where only unilateral biting was produced, despite both mandibles being in contact with the force transducer coupling. Thus the two mandibles are normally closely in phase in restrained defensive biting. This relationship can be disrupted by VMRO ablation but the effects are strongly dependent on the relative positions of the two mandibles. Phase changes usually occur at the onset of biting, relaxation typically being in phase although the reverse is sometimes found (Figure 47b). This results in the duration of the left and right bites being different within a single bilateral bite (e.g. Tables 3, 4).

(4) The strength of induced defensive biting and the influence of mandibular position

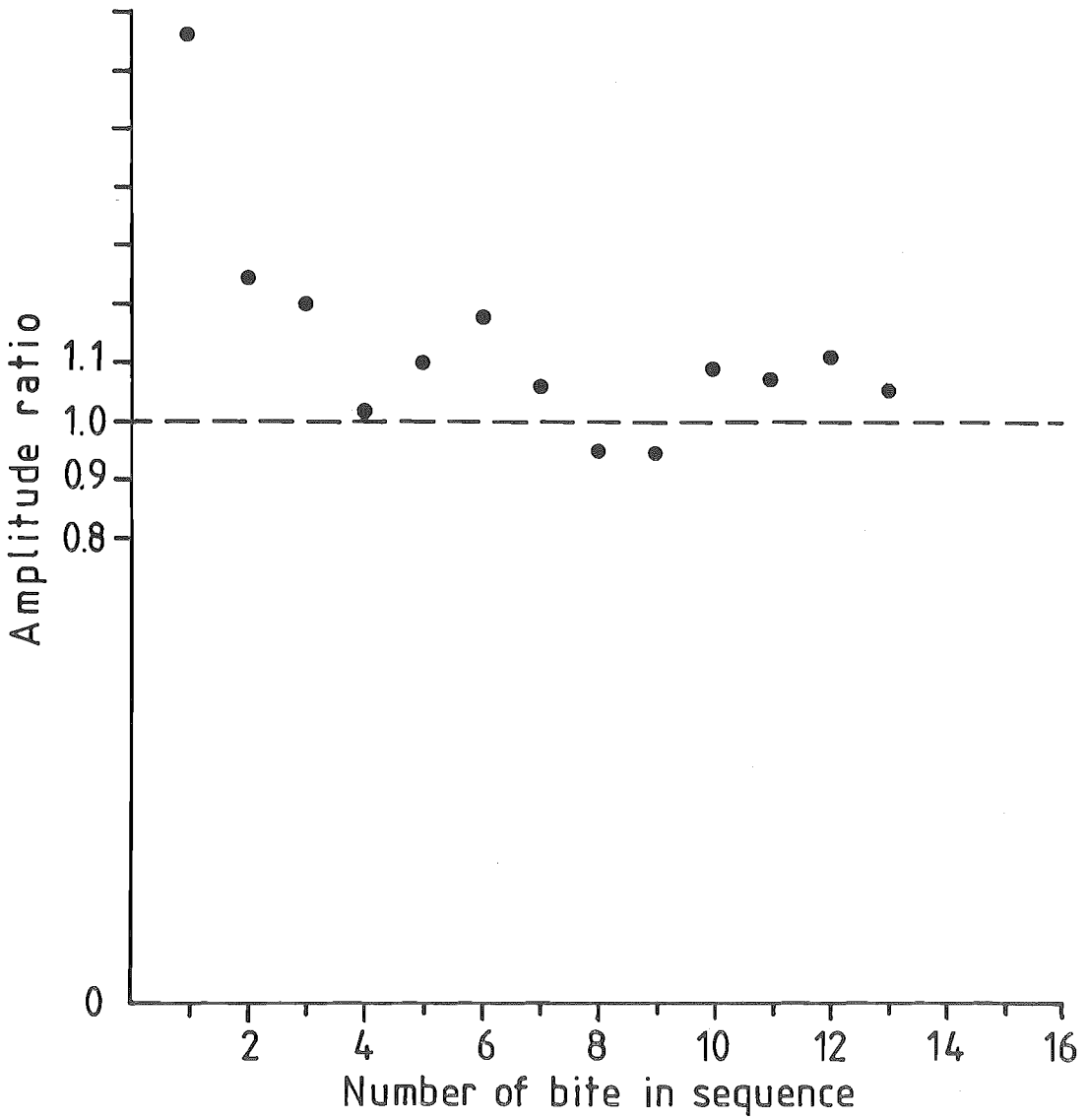
The relative position of the two mandibles influences the amplitude of bilateral bites. The use of independently-coupled force transducers creates a situation where the mandibles do not contact each other and the maintenance of position does not depend on matching of forces. It was usual to find a consistent relationship between the torque developed by the two mandibles, provided they were opened by approximately equal amounts.

Figure 48 shows a sequence of bites where the torque developed was usually but not always similar in the two mandibles. The mean ratio of right/left amplitude (the amplitude ratio) was 1.13 (905gm.cm/805gm.cm). The ratio was not always greater than one, indicating that even under the restricted conditions of a single sequence, a given mandible did not necessarily always develop a stronger bite. The right mandible was not necessarily stronger, even in symmetrically disposed mandibles, as mean amplitude ratios as low as 0.82 have been recorded.

Successive defensive bites in response to paintbrush stimulation were typically of similar strength (see Figures 44, 45) yet within a sequence there was some variation of bite strength. The trend of increasing or decreasing strength in one mandible was loosely mirrored by a similar trend in the coinciding bites of the other mandible (for example see Figure 50). Again the proviso of approximately symmetrical mandibular opening must be applied. As the imposed angles of

Figure 48

The amplitude ratio (right mandible torque/ left mandible torque) in a series of bilateral bites against the force transducers held in fixed positions.


Amplitude ratio
1.1
1.0
0.9
0.8
0
2
4
6
8
10
12
14
16
Number of bite in sequence

opening become increasingly dissimilar the ratio of right amplitude to left may alter and become progressively more variable. Both these phenomena are apparent in Table 5.

Table 5

Mean amplitude ratios (right mandible torque/ left mandible torque) during induced defensive biting in an intact animal. The right mandible is held 20° open from the rest position. Left mandible position is given as degrees open from the rest position.

Left Position	Mean Ratio	σ_{n-1}	n
17	0.99	±0.013	9
14	1.08	±0.04	7
11	1.12	±0.04	11
8	1.23	0.08	10
5	1.43	±0.24	8
2*1	7.29	±9.58	3
-1*2	16.8	±22.4	3

*1 The figures given here are calculated from the 3 bilateral bites recorded. A further 7 bites were recorded from the right mandible only.

*2 The figures given here are calculated from the 3 bilateral bites recorded. A further 3 bites were recorded from the right mandible only, and a single bite from the left mandible only.

Alteration in the geometry of the recording apparatus with progressive mandible closure accounted for a small part of the change in the ratio, but not the observed 44% change over 12° (between 17° and 5°). Nor does it

contribute to any of the increased variability in the amplitude ratio which occurs as the relative positions change. While the final two sets of figures were calculated from selected bites they illustrate several general points well. Firstly, where extremely asymmetrical positions are maintained the strengths of the left and right bites may be extremely dissimilar. Secondly, this ratio may be very erratic. These trends reach an extreme when only one mandible bites forcefully. Here the other mandible may rest against the force transducer coupling without developing any torque, or else too little to be measured accurately (amplitude ratio greater than 40, or less than 0.25). A less common finding is that the mandible is actively held open by the animal without any contact with the force transducer.

There is no absolute relationship between the amplitudes of unilateral bites and bilateral bites with the mandibles in the same position.

Measuring the force of a bilateral bite with the mandibles symmetrically disposed and then the corresponding unilateral bites reveals no consistent relationship. Unilateral bites may be greater than, equal to (see Table 6) or less than the force of the same mandible in a bilateral bite. Mean differences of 15% were exceptional and values were typically close in the two situations. The increased duration of unilateral left bites is not necessarily accompanied by a significant change in amplitude. The strength of unilateral biting was not examined exhaustively.

(5) The influence of VMRO ablation on the strength of induced defensive biting

Following VMRO ablation the relative amplitude of the two mandibles may alter during defensive biting. Table 6 gives the amplitude data for one animal (the same animal as in Table 3) before and after left VMRO ablation. The torques developed in unilateral biting were close to those recorded for the same mandibles in bilateral biting, which gave an amplitude ratio of 0.852. This changed substantialy following left VMRO ablation, due almost entirely to a reduction in the amplitude of the left mandible bite. The amplitude of the unilateral left mandible bite was approximately 25% larger than in the bilateral situation, suggesting that the ablation did not necessarily affect the amplitude as such.

The observed change appears to result from a disrupted perception of mandibular position. In attempting to calculate the post-ablation amplitude ratios for the same positions as in Table 3 it was found that bilateral biting did not always occur in any of these positions. It has earlier been mentioned that if the mandibles are held in markedly asymmetrical positions biting may be restricted to only the more widely-opened mandible. The effect of VMRO ablation is to change the relative positions in which fully coincident biting occurs. This is demonstrated in Table 7, where the tendency to bite with both mandibles expressed as the coincidence ratio, the number of bites produced by the right mandible divided by the number produced by the left. That is, there are some bites where both

mandibles were simultaneously active, and some where only the right was active.

Table 6

The effect of VMRO ablation on the amplitude of induced defensive biting with the mandibles held in constant positions. Right mandible 14° open from rest; left mandible 17° open from rest. The mean amplitude of the bites within each sequence is given in gm.cm. The amplitude ratio (AR) is the mean ratio of right to left amplitudes in each bilateral sequence.

		$\bar{x}$	σ_{n-1}	n	AR
Before ablation					
bilateral	r	1006	±43	8	0.852
bilateral	l	1180	±32		
unilateral	r	980		2	
unilateral	l	1180	±26	7	
After left VMRO ablation					
bilateral	r	1000	35	10	1.162
bilateral	l	860	55		
unilateral	r	940	47	6	
unilateral	l	1068	23	6	
After right VMRO ablation					
bilateral	r	995	14	9	1.076
bilateral	l	925	22		
unilateral	r	921	47	4	
unilateral	l	870	76	9	

Following left VMRO ablation, perfect coincidence was achieved only with the left mandible opened to much wider angles than had previously been necessary. At the given position of the right mandible a minimum shift of 18^{o} was required. While the precise values differed considerably from preparation to preparation, this surgically-induced alteration in the positions of complete coincidence was found in all preparations.

By ablating the remaining VMRO, further alteration in the positions of coincidence is induced. Table 7 shows that, in this preparation, the second ablation has reversed the asymmetrical bias created by the first. Full coincidence is now achieved only where the right mandible is held open with the left mandible close to the rest position. Again it is found that following VMRO ablation the operated mandible must be opened to a wider angle to restore fully coincident biting. With one exception this pattern was found in all preparations irrespective of whether the left or the right VMRO was ablated first. The positions in which fully-coincident biting occurs vary from preparation to preparation, particularly following ablation. A second ablation may simply negate the bias induced by the first. However, even in this case the effect of ablation shows reduced consistency between repeated tests under the same conditions.

The exceptional result of ablation referred to above occurred in a single preparation where the left VMRO was ablated first. Only one position could be found where complete coincidence was obtained.

Table 7

Coincidence ratio (number of right mandible bites/ number of left mandible bites) during induced defensive biting before and after VMRO ablation. The left VMRO was ablated first. The right mandible is held 20° from the rest position unless otherwise specified. The left mandible position is given as degrees open from the rest position.

In the lower portion of the table the left mandible is held 2° from rest and the position of the right mandible is varied. These data were obtained after the right VMRO was ablated.

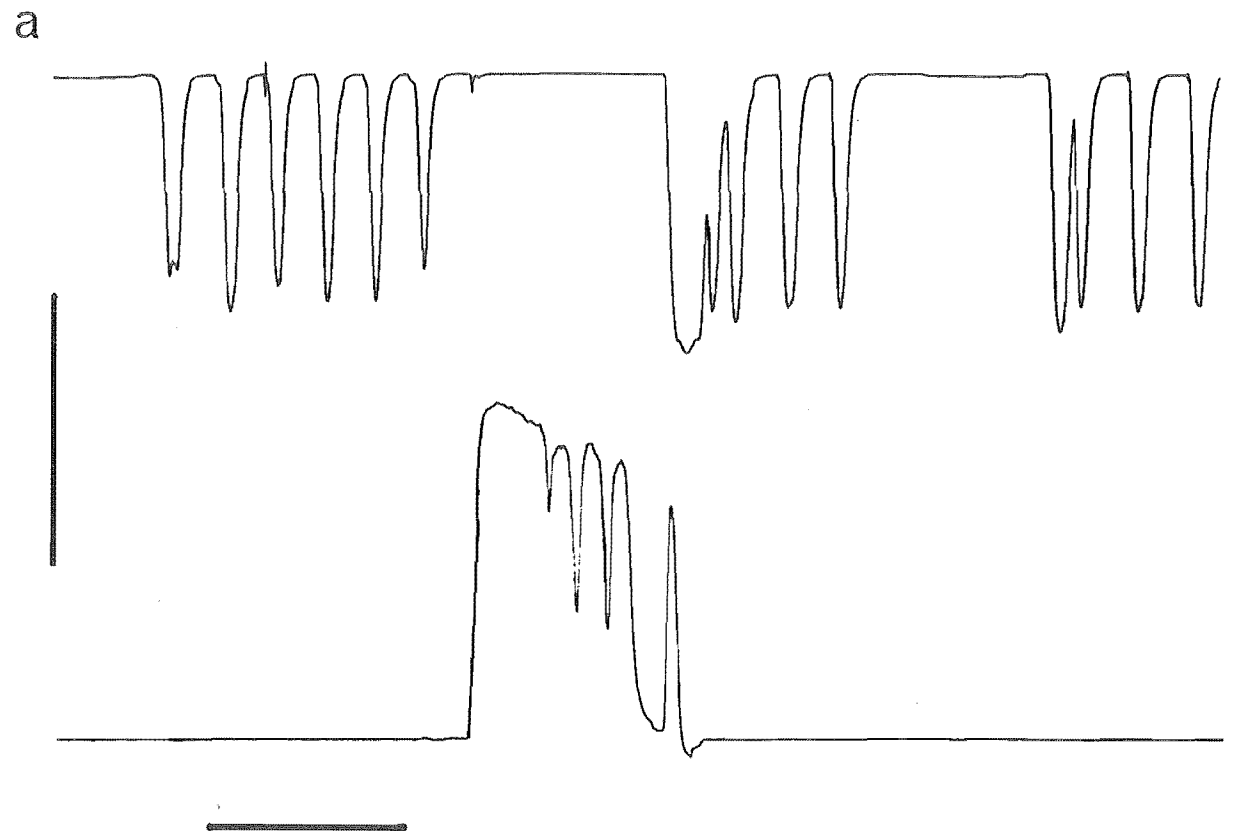
Left mandible position (degrees)	Coincidence ratio (R/L)		
	Before ablation	Left ablation	Right ablation
23	-	16/16	-
20	-	20/8	-
17	48/48	22/9	-
14	14/14	9/5	-
11	11/11	40/15	9/11
8	10/10	13/0	-
5	8/8	-	-
2	12/3	-	10/10
-1	6/1	-	-

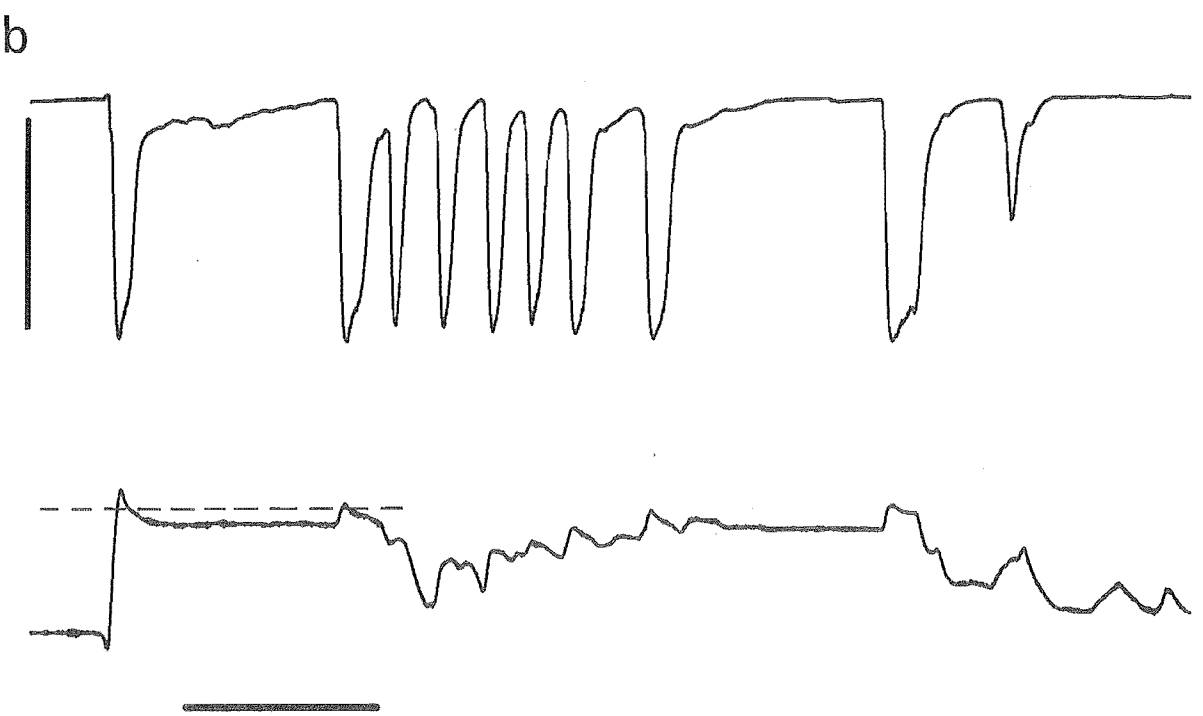
	Right mandible position	C.R
2	17	10/10
2	23	10/10
2	29	16/9

Figure 49

(a) Induced defensive biting following ablation of the left VMRO. The mandible positions are: right (upper trace) open 8^{o} from rest; left, open 15^{o} from rest. Closure is toward the midline. Vertical calibration is right mandible 900gm.cm, left mandible 1000gm.cm. Horizontal calibration: 5 seconds.

(b) Activity of the unrestrained left mandible (lower trace) during unilateral defensive biting recorded from the right mandible held 34^{o} open from rest. The initial part of the lower trace shows the left mandible held 20^{o} open from rest and then released immediately before the first bite. Vertical calibration (upper trace): 800gm.cm. Horizontal calibration: 5 seconds. The dotted line on the lower trace indicates the rest position.


a


b

A three-degree shift in the position of one mandible was sometimes sufficient to alter the biting pattern from exclusively left to exclusively right biting, although coincident biting occurred sporadically. Sequences of both right-only and left-only bites were obtained from repeated testing with the mandibles in the same position. Figure 49a shows a spontaneous change from right mandible only, to left-only, and then back to right-only all at the one position setting. Coincident bites occur at the change points, although the bite durations and amplitudes here are dissimilar. The small proportion of coincident bites decreased almost to zero following the subsequent right VMRO ablation.

Where the mandibles are approximately symmetrically disposed the amplitude ratio may be very consistent. VMRO ablation may disrupt this. Figure 50a-c shows three traces made with the mandibles in the same position. In the intact animal minor variations in amplitude of one mandible during the sequence are matched by similar variation in the other. Following ablation of the left VMRO this situation is disrupted. Fewer than half the bites recorded from the right mandible are accompanied by left mandible biting. In those that are, the amplitude ratios vary widely. The third trace shows that this is not simply an ipsilateral effect on amplitude. Following right VMRO ablation a more consistent matching of amplitude is restored, and the left mandible bites more strongly than following unilateral ablation.

The critical role of mandibular position in

determining the amplitude ratio after ablation is further illustrated in Figure 50d,e. These two consecutive traces were taken after left VMRO ablation. In the unoperated animal well-matched bites were obtained from both these positions. In trace 'e' the right mandible has been allowed to close 3^{o} more than in 'd', this being the sole difference in experimental conditions. This small shift was sufficient to alter a largely unilateral response to one where biting is fully coincident and the amplitude ratio much more consistent. Much of the apparent effect of VMRO ablation on the amplitude ratio can be compensated for by altering the relative position of the mandibles. That this can also apply following bilateral VMRO ablation is illustrated in Figure 50f, where an amplitude ratio of 1.09 ± 0.03 is found. To achieve this a grossly asymmetrical disposition of the mandibles was necessary. With the right and left mandibles respectively 23^{o} and 2^{o} open from rest only the right mandible bit in the unablated condition.

(6) The movement of the free mandible in unilateral defensive biting

The term "unilateral bite" refers to a bite where only one mandible is connected to the force transducer, the other being completely free and unrestrained. So far the activity of the free mandible has not been specified in any way. It is very seldom completely inactive, particularly in unablated preparations. While no rigid relationships between the two mandibles were

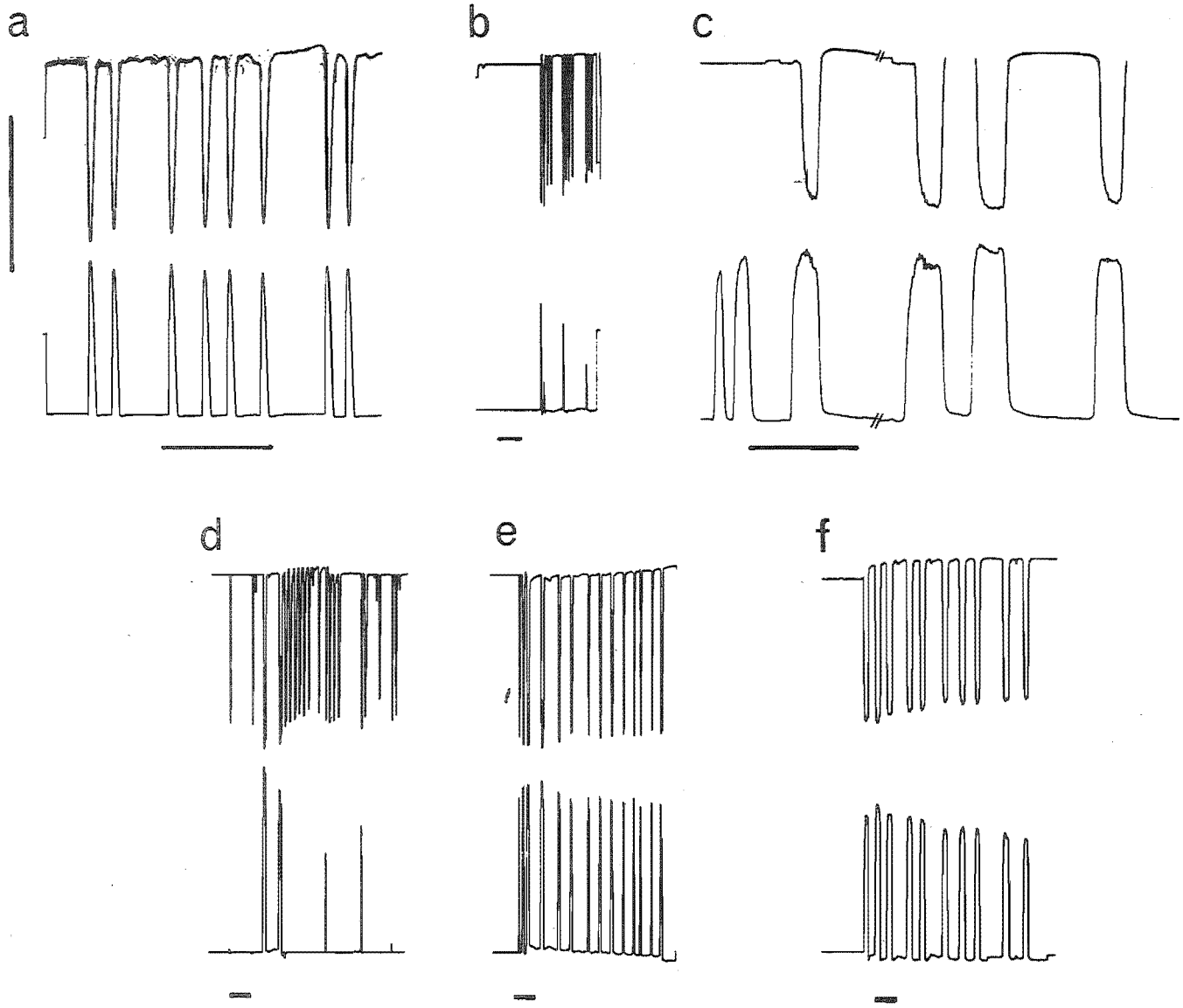
found, several trends were evident.

If one transducer coupling was removed following a defensive bite, preventing any further cusp contact, the next bite in the sequence almost invariably resulted in a rapid complete closure by the now unrestrained mandible (Figure 49b). In the absence of an apposing mandible the extent of closure is usually greater than normal, whether for right or left mandibles. The duration of the coinciding bite in the restrained mandible is frequently greater than in subsequent bites. Following a bite the unrestrained mandible may remain close to the rest position or revert to a widely gaped threat position. In either case another complete closure may occur at the next defensive bite (Figure 49b). However after the first or second bite the extent of movement of the unrestrained mandible diminishes whether the mandible remains near the rest position or reverts to the threat position. Small incomplete closure movements from the threat position, as in many of the bites in Figure 49b were commonly found. The accompanying gradual progressive closure toward the rest position from a position of threat over the course of several bites is also the typical pattern. The incomplete movements suggest that the output to the mandibular musculature is modified on the basis of previous experience. Where partial closures occur the duration of the restrained bite is usually less than in bites accompanying a complete closure. Apart from the greater tendency toward complete closure early in a sequence, it was not possible to predict the extent of

Figure 50

The effects of relative mandibular position and VMRO ablation on the relative amplitude of induced defensive biting. Traces a, b, c, were all recorded with the mandibles in the same positions: right, 20^{o} open from rest; left, 17^{o} open from rest.

(a) intact animal; (b) following left VMRO ablation; (c) following right VMRO ablation (i.e. bilateral VMRO ablation); (d) left VMRO ablated, right mandible 11^{o} open from rest, left mandible 8^{o} open from rest; (e) trace recorded immediately after d, both mandibles 8^{o} open from rest; (f) following ablation of left and right VMRO, right mandible 23^{o} open from rest, left mandible 2^{o} open from rest. Time scale: 5 seconds, in all traces. Vertical calibration: 1000gm.cm in all traces.


a
b
c
d
e
f

movement of the unrestrained mandible or the duration of the restrained bite. Within any sequence of regular, consistent stimulation the unrestrained mandible, whether left or right, tended to drift towards the rest position.

(7) Mandibular position and bite duration in defensive biting

While there is a definite relationship between bite duration and the extent of closure of the freely-moving mandible, the position of the restrained mandible also influences bite duration. This can be seen in both unilateral and bilateral biting. Where closure was almost complete, the mandibles being close to the rest position although not in contact, a prolonged bite was often observed. For example bilateral bites with mean durations of 0.37 ± 0.35s (right) and 0.51 ± 0.03s (left) were observed in a fixed position. A slight closure of the right mandible increased the duration of the right bite to 0.47 ± .07s (n = 6). The coincident left bite, with the left mandible in an unchanged position, was 0.94 ± .07s (n = 6). The great increase in duration was accompanied by a marked phase lead of the left mandible. This perhaps represents an attempt to equalise the degree of opening of the two mandibles as they approach the midline. This is a necessary condition for complete closure. Irrespective of this it is clear that bite duration and mandibular position are interdependent to an unknown extent, both in unilateral and bilateral biting.

The increased duration of bilateral biting at small angles of opening was not investigated in detail

because at these angles the couplings were often displaced by the maxillae. This does not happen at wider angles. At a varying angle of less than 10^{o} open from zero, bites of longer and less predictable duration were replaced by sequences of consistent bites with duration $D \tilde{\sim} 0.3s$. This value persisted with very little variation at all greater angles of opening in all animals. A central factor in restricting the duration within the sequences of uniformly-brief defensive bites thus appears to be prevention of the mandibles from coming close to meeting. Defensive biting can be elicited without difficulty at even the widest angles of opening. The diminished duration at wider angles of opening does not appear to represent a tendency not to bite in these positions.

(8) The influence of cusp receptors on defensive biting

As the transducer coupling contacts the richly-innervated cusp region of the mandible the possible controlling influence of receptors in this region must be considered. Hook electrode recordings from the cusp receptor nerve showed that even with the limited area of contact between the coupling and the cusp several units were stimulated. Weak active biting produced the contact force, which was much less than the maximum recorded from the heavily dissected preparation. This suggests that the stronger biting of the intact animal will always result in some sensory discharge.

Attempts to broach the cusp nerves were frequently only partially successful owing to the variability in

their branching pattern. Therefore cusp contact was circumvented by inserting a hook through the distal portion of the mandible. A chain coupling to the force transducer permitted unrestricted opening of the mandible (see Chapter II for details). Bites recorded with this apparatus had slightly lower rates of torque development and a longer duration, attributable to a small amount of stretch in both the hook and chain. The peaks of the bites were noticeably more rounded. These differences from bites onto the rigid coupling were observed both with the hook through the mandible and with the hook looped over the mandible - this latter situation was presumed to stimulate the cusp receptors during biting in the same manner as the solid coupling. Using the hook and chain coupling there were no significant differences between bite durations recorded with and without cusp contact. Both were fractionally longer than the values recorded with the solid coupling (Table 8).

The unilateral biting pattern follows the trend for the solid coupling with the right bite being similar to the bilateral value, and the unilateral left bite being substantially longer.

Phasing, too, appeared unaffected by the lack of cusp contact. In short, lack of cusp contact appears not to alter biting patterns in any way in intact animals. Even when combined with VMRO and campaniform sensilla ablation no obvious changes in rate or amplitude of torque development or phasing occurred. In these conditions the phasing and duration could be manipulated by altering mandible position as found for the solid coupling.

Table 8

The effect of cusp contact and force transducer coupling on the duration of induced defensive biting.

The duration is measured in seconds at half peak torque. All recordings were made with the mandibles as close to the same positions as possible.

Solid coupling			
	right	0.35 ± 0.03	n = 6
	left	0.41 ± 0.03	
Hook and chain on cusp			
	right	0.37 ± 0.03	n = 6
	left	0.51 ± 0.03	
Hook and chain through mandible			
	right	0.38 ± 0.02	n = 6
	left	0.47 ± 0.01	

These results suggest that cusp contact is of minor importance in determining phasing, duration and rate of torque development in defensive biting. The possibility that the very limited area of contact between cusps and transducer coupling is equivalent in these tests to total lack of cusp contact should not yet be excluded.

(9) Effect of campaniform sensilla ablation on defensive biting

In five preparations the distinct group of campaniform sensilla near the TM-muscle insertion were

ablated, either before or after VMRO ablation. In one preparation this ablation of the left mandible sensilla was accompanied by a decrease in the rate of torque development of the left mandible only. The left VMRO had been ablated. No other distinct effect of this ablation was found on the phasing, amplitude or duration of induced defensive biting.

DISCUSSION

There is little in the morphology and behaviour of the weta mandibles to suggest that the control mechanisms involved must perform any functions unique to the weta.

Apart from their increased size in mature males the mandibles of Hemideina maori are typically Orthopteran. The arrangement of the articulations and the disposition of the principal adductor and abductor are similar to others described (Strenger, 1942) although muscle M-21 is more extensively developed. Hemideina retains more of the sternal adductors (M-26 and M-25, the TM muscles) than many, which tend to have lost the equivalent of TM-2b. However Hemideina is not unique in the retention of this msucle as it is present in Locusta (Snodgrass, 1928), Dermestes (Honomichl, 1976) and Oryzaephilus (Honomichl, 1978a).

Asymmetry of the mandibles has been reported in all Orthoptera, and Hemideina follows the established pattern of having a longer left mandible. In its cusp pattern Hemideina fits the pattern described by Isely (1944) with features in common with the forbivorous-florivorous type and with the carnivorous tettigoniid Pediocetes.

The megacephaly and enlargement of the mandibles appears to have a role in agonistic behaviour, as suggested by Field and Sandlant (1983).

To achieve a strong bite with the elongate mandible the principal adductor muscle inserts at a wide displacement from the hinge line, giving a favourable mechanical

advantage for strength. Rapid angular velocities of adduction appear to have been sacrificed to achieve this, the maximum values recorded being $150^{o}.sec.^{-1}$. The high values for sarcomere length may also result from the considerable elongation many of the muscle bundles must undergo on maximal open. Long sarcomeres may allow the development of tension at greater extensions. Sarcomere lengths up to 12μm have been reported in other insect skeletal muscle (Elder, 1975) and the maximum values here are little greater (a little over 13μm). Preliminary observations of the femoral muscles of the weta (unpublished observations) indicate that long sarcomeres may be a common feature of the weta musculature, rather than a specialisation of the mandible musculature.

The range of behaviours involving mandibles extends far beyond a simple feeding role, yet none of these, with the possible exception of sound production, is peculiar to the weta. Even the distinctive threat display is found in many social insects, e.g. Myrmecia and soldier termites (Wilson, 1972) and in longicorn beetles (unpublished observations). These diverse activities are all achieved by variations in the parameters of a basically simple movement of an unjointed appendage moving within a single plane. The remainder of this discussion will concentrate on the peripheral inputs to the motor apparatus and the influence they exert on a the control of some of these activities.

The mandibles possess a diverse array of receptors, some of them peculiar to mandibles. No functional role can yet be ascribed to a number of those reported here,

including the campaniform sensilla, the other cuticular sensilla and the DMRO. The cuticular sensilla may monitor contact with food and with the other mouthparts. Particularly in an activity such as drinking, maintenance of mouthpart contact may be more important than precise monitoring of movement by internal stretch receptors (Wales, 1976).

Except around the bases of the mandible cusps the cuticular hair sensilla are sparsely distributed. Both short and long, simple, articulated hairs were found, closely resembling the pattern described for Schistocerca (Thomas, 1966). A further similarity is that the dense aggregation of large articulated hairs near the molar cusps appears not to be innervated. Both these and the shorter hairs bordering the cusps may function largely in food retention.

The powerful biting of the mandibles suggests that a safety mechanism might be found, or at least a monitor of bite force. Several candidates for such a role were found. The parts of the mandible where stresses and strains are likely to be extreme are the cusps, the two articulations and the M-21 apodeme just before it attaches to the mandible. The anterior articulation has a number of campaniform sensilla in close proximity. There are fewer at the base of the posterior articulation and the well-defined ventral group. Campaniform sensilla are known to inhibit motor neurones causing high levels of strain in Periplaneta (Zill, et.al, 1981). However, ablation of the ventral group in Hemideina had no effect on either the strength or duration of induced defensive biting, either before or after VMRO ablation.

The M-21 apodeme bears almost all the force of the most powerful bites. A nerve with numerous branches supplies the apodeme. Although the exact termination of these is not known, some branches were clearly separated from the muscle and none appeared to be intimately associated with muscle bundles (Figure 35). The endings furthest from muscle bundles are well situated to monitor total muscle tension.

Few tension receptors have been reported from insects (Burrows and Horridge, 1974; Bässler, 1977; Theophilidis and Burns, 1979). The clearly identified receptor in Schistocerca (Theophilidis and Burns, 1979) responded to tension in a restricted group of fibres in the flexor tibial muscle, rather than whole muscle output. Apodeme receptors are known from crustacea (Macmillan, 1976) and Limulus (Eagles, 1978) but their functional role is unclear. Autogenic inhibition of the associated muscle, as known in Golgi organs of vertebrates (Granit, 1950) does not appear to be the principal function of any of these receptors. However, the location of the nerves to the apodeme in Hemideina suggests such a function may be found. Some of the nerve branches approach muscle bundle insertions on the apodeme and may be in a position to monitor activity of specific parts of M-21, as was found in Schistocerca but the remainder are likely to be influenced only by whole muscle activity. A positive feedback role cannot be discounted, and the adequate stimulus is not known.

The cusp receptors responded to locally applied pressure, with increasing force recruiting more units. Responses were more phasic than found in elaterid larvae

(Zacharuk and Albert, 1978). As few units were recorded and the innervation of the cusps of Hemideina is prolific, little can be said with confidence about the receptors. The axon counts show that, considered together, the cusp receptors represent numerically the largest components of the array of mandibular receptors. Several functions are possible for receptors in this region. They may provide information about the physical consistency of the object bitten, providing positive feedback, leading to greater bite force or acting as a safety mechanism to cope with rigid objects. The force transducers used in this study would fit this category. No greater strength or duration of defensive biting was found in the absence of cusp contact, arguing against a safety mechanism. This assumes that defensive biting is an appropriate behaviour in which to look for the effects of cusp afference. The increased bite durations recorded when the mandibles were permitted to close almost to contact suggests that a positional control mechanism was terminating the defensive bites when the mandibles were more widely spaced. This may have occurred before input from the cusps, or from any other mechanism, influenced the bite.

Seath (1977a) described experiments where cautery of the cusp region inhibited synchronized adductor muscle activity when one mandible was driven and an object placed between the mandibles. Although it is not clear from his myograms what motor programme had been evoked - the closer burst was centred on peak opening - this suggests a clear role in coordination. The behaviour

of the weta following a mismatched bite may involve a similar influence. Following ablation of the VMRO, mismatched biting, where the left mandible closed inside the right, was frequently observed both in unrestrained defensive biting and in feeding (Figures 43 and 39). Particularly in feeding such a mismatching led to just sufficient opening to allow the bite to be completed with the mandibles meeting appropriately. The cusp receptors may thus be involved in determining the relative movements of the mandibles once they have made contact. In normal chewing, and in unrestrained defensive biting the movements are bilaterally asymmetrical at this stage with the right mandible displacing the left (Chapter II-1, VII-2). This is in marked contrast to the closely similar development of force found between the two mandibles in defensive biting onto the force transducer, where cusp contact was minimal, or against the hook and chain coupling with no cusp contact. The extensive innervation of the cusp region is well placed to monitor any adjustments in position or force required at the final stages of biting or to assess the consistency of the object bitten and possibly act as a safety mechanism.

The dorsal muscle receptor organ is clearly homologous with a similar receptor in Oryzaephilus (Honomichl, 1978b). The dorsal branch of the tentorial adductor is lacking in most orthopterans (Strenger, 1942; Walker, 1931; Matsuda, 1965) although it is present in Locusta (Börner, 1909). The most obvious difference

from Oryzaephilus, which also has a single motor neurone and a single sensory cell, is in the location of the dendrites. In Oryzaephilus these are intimately associated with the distal ends of the muscle fibres, whereas in Hemideina they are embedded in a collagenous matrix between the muscle fibre and the epidermis. In both animals, the dendrites are clearly in series with the muscle where they are likely to respond only to changes in receptor muscle tension. The few physiological responses are consistent with this.

While the receptor cell is clearly in series with the muscle, parallels with the locust tension receptor (Theophilidis and Burns, 1979), vertebrate Golgi organs or crustacean apodeme receptors (Macmillan, 1976) have little relevance as the sensory element is not in series with a muscle capable of moving the mandible. The DMRO appears morphologically similar to the muscle receptors described from insect legs (Markl, 1965; Bräunig, 1982).

The mandible of Homarus contains an MRO in which the dendrites of the 10-20 multiterminal sensory cells are associated with the insertion of a fine receptor muscle (Wales and Laverack, 1972a). Although insect and crustacean mandibles are not homologous, they perform similar functions in mastication in the weta and lobster, and the two have a sense organ of the same configuration.

In concentrating on the VMRO the role of the apodeme strand receptor has been overlooked. The apodeme strand receptor was found to have approximately 24 sensory cells

in a strand spanning the mandibular joint in such a way that it was stretched maximally on complete closure, as well as being coupled to the principal adductor apodeme. It appears to be homologous with a receptor in Oryzaephilus (Honomichl, 1978a). Similar concentrations of receptor cell bodies on a mandibular nerve near the base of the mandible have been frequently noted, for example, Forficula, Mallophaga, Myrmica, Periplaneta (see Bullock and Horridge, 1965). Particularly in view of the lack of tentorial adductors, and therefore muscle receptor organs, in some groups (e.g. Acridinae) this receptor deserves attention.

The most striking anatomical feature of the VMRO when compared to the other muscle receptors described, whether from insects or other arthropods, is the large number of both sensory and motor neurones. Only three of the 6-7 profiles in the motor nerve are definitely implicated as motor neurones. This number raises the possibility of inhibitory input, the utilisation of different pathways in different activities (fast or slow contractions) or a collateral innervation with the TM-1 muscle, as in the β-innervation of the vertebrate intrafusal muscle spindle (Murthy, 1978). While most arthropod muscle receptors have only one or two primary units, the number of sensory neurones in the VMRO is no larger, than found in a number of chordotonal organs. Approaching 400 were found in the proximal scoloparium of the femoral chordotonal organ in the grasshopper (Moran et.al., 1975).

Many of the VMRO dendrites terminate within the receptor muscle, some of them definitely at the level of the Z-discs, thereby creating the possibility of a response to tension within the receptor. Other sites for dendritic termination, cannot be excluded and there may be receptors both in series with the receptor muscle and in parallel with it.

The muscle fibre tract is an anastomosing network but it is not known how many discrete elements may be present within it. Muscle fibres with a dissected profile seen in transverse section may still remain distinct from other fibres.

In its structure the VMRO is closely similar to the muscle receptors described from mandibles in the beetles Dermestes and Oryzaephilus (Honomichl, 1976, 1978a). The differences are largely in scale, Dermestes having about ten sensory neurons and Oryzaephilus eight. While these eight are clustered near the origin of the muscle, its small size, about 100µm, suggests that this is not a fundamental difference. In other anatomical details, including the structure of the muscle fibre tract, the lack of ciliary contents of the naked dendritic endings and their termination in the region of the Z-discs, the receptors in the weta and the beetles are essentially the same. One fundamental difference possibly exists. In Oryzaephilus dendritic endings free from the muscle fibre tract have been reported, whereas their existence in Hemideina is unconfirmed.

Anatomical differences from other insect muscle receptors are pronounced. Stretch receptors associated

with muscles in the thorax or abdomen have been described from six insect orders (Finlayson, 1976) some are associated with skeletal muscle and some have developed specialised muscles independent from the ordinary body musculature. They all have only one or two sensory neurons. Few have been investigated ultrastructurally. In the moth Antheraea, the single receptor cell has multiple dendritic endings in a specialised fibre tract lying alongside the receptor muscle fibre (Osborne and Finlayson, 1965). Features in common with Hemideina include multiterminal dendritic endings devoid of ciliary contents and free from glial cell covering.

Muscle receptors have been identified from the legs of four insects. In the honey-bee (Markl, 1965) and Locusta (Bräuing, 1982) a specialised receptor muscle with a single cell body spans the coxa-trochanter joint. In Carausius (Bässler, 1977a) and Schistocerca (Theophilidis and Burns, 1979) a single multipolar cell sends dendrites into the distal bundles of the flexor tibiae muscles of some of the legs.

This has been shown to monitor muscle tension in the pro- and mesothoracic legs of Schistocerca. Although the ultrastructure of these receptors has not been described they all resemble the multipolar cells of abdominal stretch receptors (Finlayson, 1968). Their dendritic terminations are unknown and in each case may be in series with either the skeletal muscle fibres, as in the femur of Schistocerca or the receptor muscle as in the honey bee, and locust coxa and the DMRO of Hemideina.

The sustained excitatory responses recorded on imposed opening of the mandible suggest that the VMRO has many position sensitive units, although a tonic response to an increase in passive tension following stretch would give a similar response. The almost total loss of activity that invariably followed motor nerve section implies that the types of unit seen in Figures 28 and 30 are not simply length sensitive, nor are they responding to a stretch-induced increase in passive tension. The bursty nature of the discharge in Figure 28 suggests a motor influence. Reflexively-induced inhibition of the right VMRO by left mandible opening confirms this. To determine the relationship between VMRO output and receptor muscle length and tension it would be necessary to control and monitor these parameters in a preparation where the receptor insertion is detached from the mandible. Experimental control of the motor input would be advantageous. While acknowledging the difficulties of interpreting responses when the set-point of the receptor is not controlled, it appears that the VMRO may well be responding to change in its own internal tension. The bursts of discharge in synchrony with TM-1 myogram activity (Figure 29) resemble the short bursts seen in Figure 28c-e. The location of the dendrites at the Z-discs of the receptor muscles effectively places them in series with the contractile elements, although the limits of the transduction zone within the dendrites are not known. A series arrangement is necessary for tension reception. This implies that some other afference is stimulating the motor input to the receptor. In considering this possibility it is

interesting to note that the large unit in Figure 30 showed a sustained discharge to maintained stretch, yet showed no phasic discharge during active stretch to this position. However, it produced phasic bursts while in a constant position at a lesser angle of opening.

The necessary positional information could come from within the VMRO or from another source such as the apodeme strand receptor, or from position sensitive units within the VMRO. Small units firing tonically are evident in Figure 28d and 29a. A small movement and position sensitive unit continuing to discharge following motor nerve section is seen in Figure 30b.

The sporadic bursts of higher frequency discharge from larger units found in various traces in Figures 28 and 31 presumably results from phasic changes in motor input. The appearance of these out of phase with other activity suggests that there may be functionally separate components within the receptor, possibly involving separate muscle fibres with different innervation, as in some of the crustacean MROs (Fields, 1976).

An inhibitory effect of contralateral mandible opening on right VMRO discharge is clearly evident in Figures 28 and 31. The result of sectioning the left VMRO nerve suggested that most but not all the inhibition came from the VMRO. It is possible that the VMRO was solely responsible. While the sensory nerve was cut, the motor nerve was not. This has been shown to contain 6 or 7 profiles, of which at least three are probably motor neurones. The others may be sensory. The alternative is a muscle receptor with a large and

variable number of motor neurones. Even if the extra 3-4 neurones are sensory they are not necessarily the source of afference leading to right VMRO inhibition. Receptors associated with the cusps or the other stretch receptors, the DMRO or apodeme strand receptor could provide the necessary input.

The right VMRO discharge was least when both the right and left mandibles were closed. It was excited by imposed opening of the right mandible. Most units were then inhibited by imposed opening of the left mandible. Discharge from many units in the right VMRO was least in positions where the mandibles were symmetrically disposed, suggesting strongly that many of the receptors are not simply position sensitive. Another possibility is that the receptors are responsive to length change but subject to inhibition at the periphery as described from crayfish thoracic muscle receptor organ (Eyzaguirre and Kuffler, 1954). This might account for the number of motor neurons (at least 3, possibly 6) to the receptor. Morphological correlates of receptor cell inhibition were not found. Tension-sensitive responses could be inhibited peripherally by an inhibitory motor neuron, central inhibition of the receptor motor neurones is the third possibility.

In all of these proposals the receptor is functioning as an error detector. While some units may respond to tension within the receptor muscle, the situation of the receptor in parallel with the skeletal muscle prevents direct monitoring of skeletal muscle tension.

In their lack of a consistent response to length change, most of the VMRO units recorded do not resemble

the responses recorded from abdominal MROs in either Rhodnius (Anwyl, 1972) or in larval and pupal Antheraea (Weevers, 1966a). A slight intrasegmental crossed reflex was recorded in Antheraea (Weevers, 1966b).

Interpretation of the responses recorded from the VMRO is complicated by both the number and variety of units and the dependence of many of the responses on an intact motor supply. This latter factor suggests that considering the sensory responses in isolation from the activity of the muscles they control may not be meaningful. If the VMRO functions as an error-detecting element in a servo mechanism then its responses are best considered with respect to the ongoing motor programme. Both the abolition of the phasic and some tonic activity following motor nerve section (Figure 30) and the coincidence between phasic VMRO discharges and the TM-1 myograms, suggest a servo function. The positioning of the VMRO in parallel with the TM-1 musculature further supports this idea. This "in parallel" configuration closely resembles that of the vertebrate intrafusal muscle spindle, a receptor under efferent control and known to perform an error-detecting function (Matthews, 1972; Houk, 1979).

In considering this possibility the number of sensory units, perhaps 150, and the diversity of their responses should be kept in mind.

The large number of units and the small physical dimensions of many of them means that many units may not have been recorded from, for example, tonic position-sensitive units. Such a possibility must be kept in mind when attempting to explain the behavioural changes

resulting from VMRO ablation in terms of known receptor physiology.

The existence of muscle receptor organs within the tentorial adductor muscle blocks rather than in parallel with the principal adductor seems less surprising when it is remembered that the homologous tentorial muscles are the major functional adductors in the thysanuroid type of mandible (Matsuda, 1965) which has a unicondylic articulation. When present in the Pterygota, the tentorial adductors are generally considered to be vestigial remnants of these same adductors (Snodgrass, 1950; Matsuda, 1966; Manton, 1964). The trend toward reduction in the number of mandibular muscles reaches its limit in the Acridinae where only a single adductor (m-21) and a single abductor (M-23) are present (Strenger, 1942;Snodgrass, 1928). However, insects from a number of orders possess a single tentorial adductor closely similar in size and appearance to TM-1 in Hemideina maori. These include Blatta (Snodgrass, 1950), Grylloblatta (Walker, 1931), Mantis and Decticus (Strenger, 1942).

Presumably those insects which have only muscles 21 and 23 do not possess muscle receptor organs and may have radically different sensory systems, perhaps based on the apodeme strand receptor. In the light of the evolutionary trend toward reduction of the mandibular musculature, it is surprising to find the two receptor muscles retained in such divergent taxa as the Stenopelmatidae and the Cucujidae (Oryzaephilus).

Morphological homologues of both these muscles have been figured for Locusta (Börner, 1909, in Snodgrass, 1928) and a tentorial adductor is found in certain biting Diptera (Tabanidae reported in Snodgrass, 1950). Careful investigation of mandibular stretch receptors would determine the presence or absence of muscle receptor organs and indicate the variety of solutions to the problems of feedback control of mandibles.

In the remainder of this discussion an attempt is made to reconcile the experimentally tested behaviours with the known properties of the sense organs.

The weak closure responses occurring immediately after the application of loads to the inactive animal (Figure 41) suggests that a posture maintaining system is operating. Several observations are consistent with such a mechanism involving the TM-1 muscle and the VMRO. The two are closely in parallel so that changes in the length of the muscle are in direct proportion to changes in the receptor length. The TM-1 muscle is known through myography (Figure 21) to be active in the weakest mandible movements, with little apparent involvement of muscle M-21. Strong resistance reflexes were obtained from TM-1 in response to imposed mandible opening (Figure 22) while resistance reflexes were often difficult to elicit from M-21. Should TM-1 be exclusively involved then the system would probably not be able to compensate fully for loads of more than 3-4gm.cm. Loads

of this magnitude were not tested, but partial compensation was observed with larger loads, perhaps implying M-21 involvement. Tonic responses to maintained mandible opening have been recorded from the VMRO. So too have phasic responses in synchrony with phasic muscle activity in TM-1 (Figure 29b). In these the onset of muscle activity slightly preceded the sensory response, ruling out the possibility that the phasic sensory afference elicited the phasic muscle burst. However, it is possible that tonic output from the VMRO, or perhaps the apodeme strand receptor, signals the movement of the mandible, activating both the TM-1 and the VMRO motor neurones. Obstruction of any closure movement could then be monitored by an error signal from the VMRO, accounting for synchrony in the phasic responses. Autogenic reflexes such as this have been described for several receptors under efferent control, such as the thoracic-coxal muscle receptor in crabs (Cannone and Bush, 1981).

The responses to loading the mandibles during feeding activity showed that the extent of opening was not regulated completely, if at all. Even 15gm.cm loads caused appreciably larger angles of opening. Despite this, cycle frequencies were maintained under both unilateral and bilateral loads. The loads applied, while not completely compensated for when applied to the passive animal, were approximaely 1% of the maximum possible adductor muscle output. Such variations in load would presumably be found within the variety of foods normally taken and be dealt with by increased closer

muscle output as described in Schistocerca (Seath, 1977b) and Homarus (Macmillan et.al., 1976b). Load variation caused by differences in the feeding substrate takes effect when the mandibles contact the food and represent a different situation from a constant load applied throughout the bite cycle. Unilateral weighting caused a difference in opening angle in the two mandibles (Figure 42), yet coordinated chewing was maintained without mismatching of bites. This requires a load-compensation mechanism to be active in regulating mandibular position before there is any mechanical coupling of the mandibles from either cusp contact or via a food bolus. Position was not completely regulated throughout the cycle but symmetry of position between the mandibles was reached at the end of closure. A position comparator is implied. The reflex excitation of the VMRO in the more widely opened mandible by afference from the more closed mandible (Figures 28 and 31) suggests that the VMROs are well suited to such a mechanism.

The difference between the precise regulation achieved under a unilateral load and the incomplete closure movements resulting from loading the quiescent animal suggest that the extent of load compensation depends more on the ongoing motor programme than it does on the receptor output. Of course, if the VMRO is involved, receptor output is also likely to be determined by the ongoing motor programme.

In attempting to determine the functional role of sense organs by examining alterations in behaviour

following their ablation the nature of the ablation must be considered. The observed effects may vary with the ablation technique. Complete removal of proprioceptors may have little influence on stick insect leg movements, particularly in comparison to producing "incorrect" afference (Bässler, 1977a).

While the operation of releasing the distal end of the VMRO has throughout the text been referred to as an ablation, the receptor was not extirpated as this term might suggest. At most only a small proportion of the sensory units were likely to have been damaged in the operation, in which the nerve connexions were left intact. Unless the release of muscle tension and subsequent shortening totally inactivated all the sensory units, it is likely that the VMRO continued to send input into the central nervous system. It is not possible to say how any such information might be related to efferent activity or to mandible activity save that responses denoting extreme value of either tension or position would presumably be lacking. As the receptor is possibly active the ablations cannot be considered strictly equivalent operations in different animals.

Two features recur as effects of VMRO ablation in various behaviours - disruption of the perception of position, and comparison of the output of the two mandibles. In feeding behaiour (Figure 39d,e) the angle of opening of one mandible diminished following unilateral ablation in one animal. The ablation operation

permits shortening of the receptor, difficult to reconcile with a decreased angle of opening. Subsequent left VMRO ablation not only restored the balance but increased closure in the left mandible causing mismatched biting, where the mandibles did not meet appropriately. Both the ipsilateral and contralateral mandibles again suggest a comparison between the two has been involved.

Similar mismatching in defensive biting commonly followed VMRO ablation while some of the results were consistent with an underestimation of opening, for example the mismatching resulting from the too rapid closure of the left mandible in defensive biting (Figure 43b). Mismatching of bites sometimes occurred only following bilateral ablation. The only safe conclusion is that VMRO ablation disrupts the estimation of relative mandible position and may have both unilateral and bilateral effects. In discussing the loading experiments an error detecting role in load compensation was proposed for the VMRO. The reason for now proposing a position-sensitive role is that, particularly in defensive biting, the only load is that of the mandibles themselves. By the time additional loads are added (in cusp contact) the mistake in position perception has already been made.

It is argued later that defensive biting is a ballistic manoeuvre where the increase of bite force is not initially under the control of peripheral feedback. Can the mismatching resulting from VMRO ablation be reconciled with the possible ballistic nature of defensive biting? If an assessment of mandible

position prior to the bite is made even partially on the basis of VMRO output, errors in occlusion are likely to result from VMRO ablation.

In other preparations more equal opening was observed but the chewing cycle appeared more irregular. While these behavioural changes cannot be related even qualitatively to changes in receptor length following ablation they constitute a clear disruption of positional control.

The approximately symmetrical mandibular opening required before bilateral defensive bites are produced may be monitored by a similar mechanism to that proposed to account for the weak load compensating behaviour. Bilateral bites were produced at all angles of opening, provided the two mandibles were opened approximately symmetrically. Clearly the relative position of the two mandibles is monitored in some way. The reflexive inhibition of right VMRO discharge by left mandible opening (Figures 38 and 31) provides a mechanism by which such a comparison could be made. The involvement of the left VMRO in this inhibition is completely consistent with the disruptive effect of VMRO ablation on the positions at which completely bilateral biting (coincidence ratio, 1/1) was found.

Changes in the phasing of induced defensive biting can result from VMRO ablation (Figure 46) and can subsequently be altered by the changing position of either mandible.

Similarly in induced defensive biting the relative force produced by the two mandibles can be drastically altered by VMRO ablation (Figure 50) although each

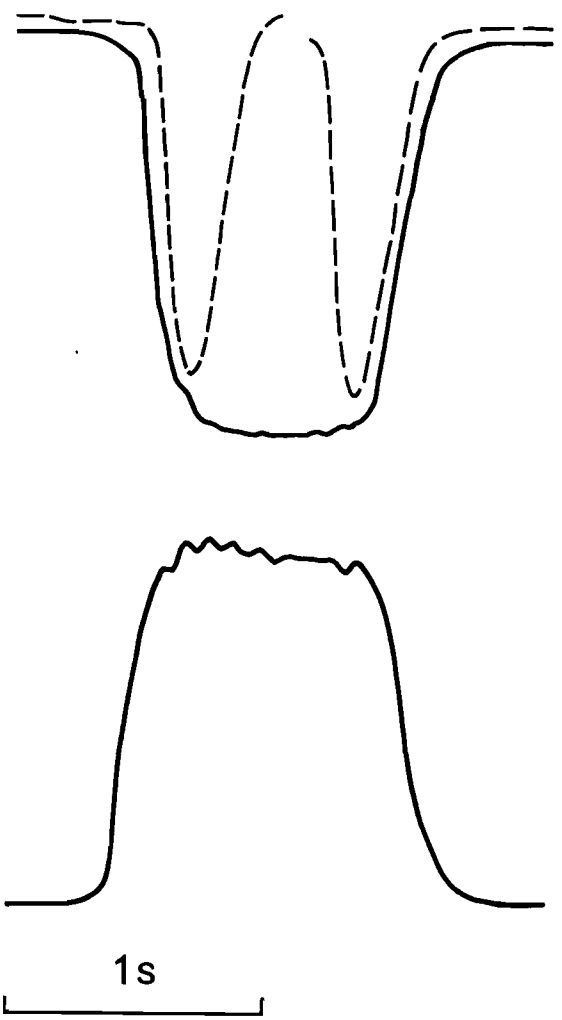
mandible can produce strong unilateral bites in the test position. Following the ablation the relativity between the two mandibles may be restored by changing their positions (Figure 50).

Induced defensive biting against rigid transducers produced large numbers of bites of a highly consistent type. These were characteristically strong (>800gm_cm(and brief (0.25-0.4s duration at half peak tension). Bites of this description were not obtained when the transducers were rigidly mounted in position allowing the mandibles to close almost completely. Longer bites occurred in this situation (Chapter VII-7). It is proposed that the attack bite is partially a ballistic manoeuvre, inhibited by positional information indicating failure to close when the maximum force has been produced. The highest angular velocities of closure were recorded during unrestrained defensive biting. The most rapid bites against the force transducer were defensive bites. The rate of torque production as revealed by the slope of the pen-recorded traces, was uninfluenced by elimination of several sources of sensory input. Ablation of the ventral group of campaniform sensilla had no effect on induced defensive biting. Nor did the presence or absence of cusp contact. The slopes of the force transducer traces were the same before and after VMRO ablation following defensive biting induced by stroking with a paintbrush (Figures 44 and 51). In contrast, voluntarily produced bites were slower and irregular (Figure 44g). Together these

Figure 51

Induced defensive biting before and after VMRO ablation.

The solid lines show the force transducer output recorded during a bilateral bite after the ablation of both ventral muscle receptor organs. The dotted lines show two superimposed bites from the same animal recorded before ablation.


1s

factors are evidence for a ballistically-initiated bite as has been reported in some mammals (Weijs, 1980). The short duration of the bite appears to result from the inability of the restrained mandibles to close. As various parameters increased bite duration without apparent increase in bite strength a tension monitoring mechanism is not indicated. VMRO ablation increased duration (Tables 2 and 3) although this receptor is not placed to monitor adductor muscle tension. Ablation did not alter the rate of torque production (Figure 51) or strength of bite (Table 6). Longer unilateral bites were produced when one mandible closed appreciably (Chapter VII-6). Strong sustained biting of soft objects has been noted.

In advocating a dependence on positional information it is the position of the mandible which is referred to. The units of the VMRO inhibiting the defensive bite at peak torque may well be responding to extremes of tension within the receptor muscle, resulting from obstruction of mandible closure. Following VMRO ablation the error signal would not be produced and the full strength of biting sustained.

While VMRO input can readily be shown to affect the duration of induced defensive biting, the effects of input from the left and right receptors are not equal.

The right mandible appears to be exerting a dominant influence over the left. The durations of unilateral right and bilateral bites are similar, and longer than the left unilateral bites (as in Tables 2 and 3). Ablation of the right VMRO resulted in

increased durations of both right and bilateral bites. Unilateral left VMRO ablation had little effect on many bilateral bites in all preparations, despite pronounced increases in the durations of the left unilateral bites.

These effects were recorded where the mandibles were restrained and not coupled to each other. In free chewing the two mandibles have different patterns of movement, with the right moving more in the final shearing phase of biting (Figure 3a). This asymmetry in movement may have led to the development of differential effects of the two VMROs. The possibility of differences between the two sense organs has not been examined.

To determine the role of a proprioceptor from ablation experiments it is necessary to choose an appropriate activity. A behaviour may not necessarily be strongly influenced by all the sense organs stimulated by it. In examining cheliped flexion behaviour in hermit crabs, Field (1976) found that one effect of ablating the CP1 chordotonal organ was an increase in cycle time and burst duration. Ablation of the CP2 chordotonal organ had no significant effect on the motor programme, although a resistance reflex was eliminated.

The altered bite duration and position-related effects resulting from VMRO ablation have largely been derived from observations on defensive biting. If this behaviour is not subjected to peripheral control in all its stages many proprioceptive inputs from the

VMRO and other receptors may not have been expressed. Extending the range of behaviours examined would provide further insight into the unique problems of mandibular control.

The weta mandibles are asymmetrical both in their movements and their morphology. By their apposable action the movement of one directly affects the other. Biting requires the precise meeting of the mandibles and the synchronised production of strong forces.

The large array of proprioceptors in the weta mandible includes a complex stretch receptor under efferent control. This unique structure may have developed in response to the peculiar requirements of the biting mechanism.

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